THE LIFE HISTORY OF SPERM WHALES, *Physeter macrocephalus*, FROM SOUTHERN AUSTRALIAN WATERS

by

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STATEMENT OF ORIGINALITY

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

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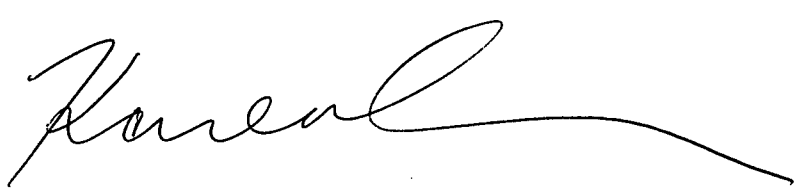

Karen Evans
11 June 2003

In memory of

Terence Bernard Evans

ABSTRACT

One hundred and fifteen sperm whales (97 female, 15 male, 3 unknown gender) were involved in three mass stranding events during the month of February 1998 along the west and north-west coastlines of Tasmania, Australia. Sixty six of these whales stranded at Ocean Beach, Strahan, 35 at Greens Beach, Marrawah and 11 at Black River Beach, Stanley. The remaining three whales stranded singly along the coastline. Three mass strandings of this species in such close temporal proximity have not been reported in this area before, and this is the first time that samples have been systematically collected from complete or near-complete groups of sperm whales from Tasmanian waters. The broad aim of this project was to examine the life history of complete or near complete female groups of sperm whales in an effort to contribute to the paucity of knowledge on two key areas of research identified for sperm whales in the Australian Government's Action Plan on Australian Cetaceans: the basic biology of this species and pollutant impacts on this species.

This study is made up of three components: (i) by developing modifications to current methods of age determination, an assessment of the demographics and growth of the female component of these groups was undertaken; (ii) by collecting stomach contents and blubber samples, an investigation into energy acquisition and storage was undertaken and (iii) concentrations of organochlorines were determined from blubber samples and concentrations and interpreted in light of ecological factors such as diet and demography.

The three stranding groups were composed primarily of adult females. Total lengths of all animals ranged from 417-1200 cm and ages ranged from 0.75-64 years. Female sperm whales, unlike many other mammals, demonstrate high, relatively stable survival throughout their entire life span. Overall, growth is prolonged in female sperm whales, not reaching asymptotic length until around 20 years. The longevity, low fecundity, slow growth, delayed sexual maturation and high input of resources into young over a protracted period define sperm whales as extreme K-selected animals. Survival in mature female sperm whales in this study was higher than those observed in mature females from Japanese waters and similar to that observed in female sperm whales deriven from Western Australian whaling operations. This suggests survival in female sperm whales from Australian waters may have undertaken little change post whaling. However, there appear to have been some changes in the age structure of female sperm whale groups and additionally increases in the total lengths of individuals, which indicate some post-whaling demographic changes.

The diet of southern Australian sperm whales in late summer was dominated by oceanic cephalopods. Cephalopod beaks from stomach contents represented 48 species from 14 families of Teuthids, two species from two families of Octopods and the single Vampyromorph species. Subtropical and muscular species of cephalopods dominated the diet of southern Australian sperm whales, but a high level of both inter- and intra-group variability in the diet was apparent. Common cephalopod prey species were similar to that of sperm whales elsewhere in the Southern Hemisphere and included members of the Histioteuthidae, Onychoteuthidae, Ommastrephidae, Architeuthidae, Cranchiidae and Pholidoteuthidae families. While smaller species (<300 mm dorsal mantle length) were numerically abundant, larger species (>1,000 gm) were clearly important to sperm whales (comprising 78.6 % of the total estimated wet mass) and are likely to provide an efficient means of acquiring energy for this species. Differences in diet composition and prey size between sperm whales reflect individual variability in foraging success and perhaps also foraging groups related to the social structure of this species.

Individual variability in foraging success and therefore, in the acquisition of energy will be reflected in an individuals energy stores. High individual variability characterised both blubber thickness and blubber lipid content in the sperm whales in this study, which suggests both deposition (acquisition) and mobilisation (utilization) of energy stores differed between individuals. The social structure and foraging ecology of this species may serve to minimize the need to rely on stored energy reserves to meet reproductive energy requirements. Continual foraging of lactating mothers facilitated by communal care of young by other members of a pod would aid in facilitating flexibility in the acquisition of energy in an effort to meet energetic costs associated with reproduction, minimising the need to draw on energy reserves to meet those demands. Additionally, the broader role of blubber for structural, buoyancy and insulative functions coupled with high individual variability may cause a lack of obvious relationships between these variables and body size, age, sex and reproductive state in this species.

Organochlorines were present in the blubber of all sperm whales sampled in this study. The relationships between organochlorines, sexes, age and reproductive groups were marked by high individual variability and highlight the complexity of organochlorine accumulation in this species. Differences in organochlorine concentrations were observed between two stranding groups and are likely to be the result of differences in the dietary composition and foraging areas of the groups. As a result of this smaller geographic scale of variation, it is therefore difficult to determine temporal changes in

organochlorine concentrations positively in highly mobile species across large regions. Organochlorine concentrations were on the whole lower than those observed to be linked with deleterious effects in cetacean species elsewhere. However, it is difficult to draw clear conclusions from this due to species-specific intake, differences in metabolism and differences in physiological reactions to pollutant concentrations.

A life history involving low fecundity, high longevity, slow growth rates and delayed attainment of sexual maturity, a high input of resources into young, and high sociality involving communal care of young and communal defense all under-pin the aspects of the life history sperm whales observed in this study. Yet despite the high dependence on life as a social "unit" this study highlighted the influence of individuality on the life history of female sperm whales. The sociality of female sperm whale groups allows for flexibility in life history traits providing these animals with individual means to sustain their fitness in an aquatic environment and allows them to ride out temporal and geographical fluctuations in the environment. The identification of present day threats and their impacts on sperm whale populations (*e.g.* chemical and noise pollution, competition with fisheries), moreover establishing the identity and interactions between sperm whale populations in the Australian region, are essential for determining current pressures on populations and should be a high priority for environmental managers in ensuring the conservation of this species.

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Finally, this one goes out to you Patricia, thanks for all your support, encouragement and faith.

The following publications are derived or partly-derived from research associated with this project:

Evans, K. (In Press). Pollution and marine mammals in the Southern Hemisphere. Present or potential threat? In N. J. Gales, M. A. Hindell and R. Kirkwood (eds.). Marine mammals. Fisheries, tourism and management issues. CSIRO Publishing, Melbourne.

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Evans, K., Morrice, M., Hindell, M. and D. Thiele. (2002). Three mass strandings of sperm whales, *Physeter macrocephalus* in southern Australian waters. Marine Mammal Science 18(3): 622-643.

Evans, K. and K. Robertson. (2001). A note on the preparation of sperm whale teeth (*Physeter macrocephalus*) for age determination. Journal of Cetacean Research and Management 3(1): 101-107.

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. Behavioural and Brain Sciences 24(2): 346-347.

Mesnick, S. L., Evans, K., Taylor, B. L., Hyde, J., Escorza-Treviño, S., and A. E. Dizon. (2003). Sperm whale social structure: why it takes a village to raise a child. Pages 170-174 in B. M. D. Wall and P. L. Tyack (eds.). Animal social complexity. Intelligence, culture and individualized societies. Harvard University Press, New York.

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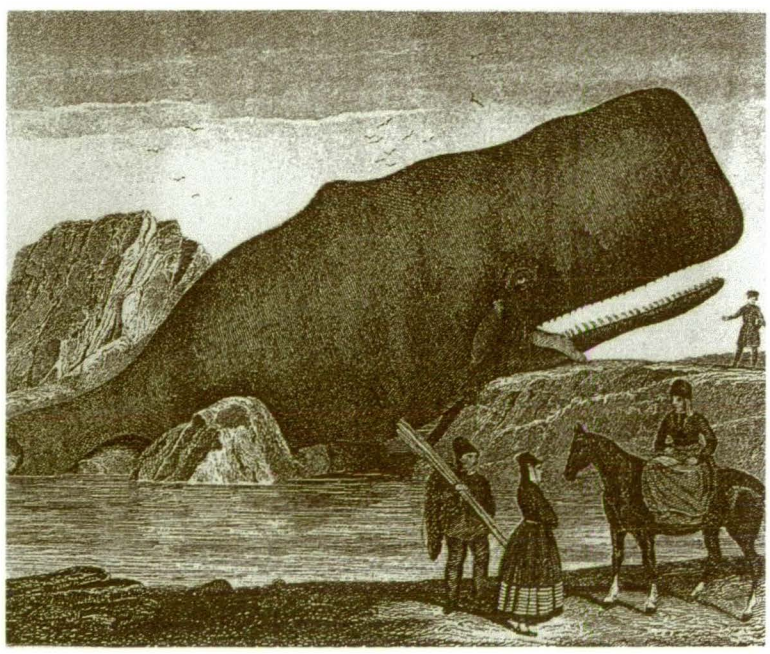

CHAPTER ONE

GENERAL INTRODUCTION

1.1. BACKGROUND

1.1.1. The species

1.1.1.1. Demography

The sperm whale (*Physeter macrocephalus*) is the largest of all the Odontoceti (toothed whales) and is characterized by the greatest sexual dimorphism of any cetacean (Whitehead and Weilgart 2000), with males attaining total lengths of 18 m and females reaching 12 m (Rice 1989). Sperm whales demonstrate slow growth rates and slow attainment of sexual maturity, which in females occurs at around ten to 13 years, [although pregnancy had been reported in animals as young as seven years (Best *et al.* 1984)] and in males at around 18-21 years (Rice 1989). Physical maturity is not attained until 25-45 years in females and 35-60 years in males (Rice 1989) and life spans can reach 70-80 years (Ohsumi 1966).

The reproductive strategy of this species is typified by low fecundity. The average reproductive cycle of a female sperm whale is in the order of four to six years and involves a gestation period of 14 to 16 months, followed by a lactation period of approximately two years. Calves are completely dependent on milk produced by their mothers until their second year when milk intake is supplemented by solid food. However, lactation may continue for a number of years (Best *et al.* 1984), but is thought in these instances to be related to the development of social bonds rather than strictly providing nutrition (Boness *et al.* 2002). Resting periods between reproductive cycles are thought to be between 0.75-2.75 years, and subsequently, a female might be expected to produce only four to five calves in her lifetime (Best *et al.* 1984). Given this low fecundity rate, ensuring calf survival is of extreme importance and subsequently, maternal inputs of energy and time per offspring are high.

1.1.1.2. Social structure and distribution

The sociality and distribution of this species also exhibits sexual dimorphism. Females and their calves associate socially in groups of ten to 30 individuals. These groups consist of dynamic associations between two or more stable units of around 13 animals which themselves are based on mixed matrilines and long-term associations (Whitehead *et al.* 1991; Christal and Whitehead 2001; Mesnick *et al.* 2003). The relatedness of these units suggests that the large proportion of females probably remain with their close relatives for long periods, if not for their entire life (Whitehead and Weilgart 2000). The primary benefits of such associations between female sperm whales are thought to be associated with communal defense against predators, communal care of young and co-operation in the location and capture of prey (Whitehead 1989; Richard *et al.* 1996; Christal and Whitehead 2001). It can therefore be postulated that the importance of these social groups appears to centre on ensuring survivorship of offspring.

Males conversely, disperse from their natal groups. It is not clear at what age males dispersal occurs and has been reported to occur at six to ten years (Best 1979; Richard *et al.* 1996) and around 15 years (Rice 1989). On leaving their natal groups males associate with others of a similar size rather than age group, with groups observed to contain 12 to 15 individuals (or multiples thereof) ten to 29 years in age (Best 1979). However, mixed schools of immature males and females have been reported from whaling data and suggest limited female dispersion from natal groups. As males grow, the aggregations they are associated with become less concentrated and eventually mature individuals become largely independent of each other (Best 1979; Whitehead and Weilgart 2000). The movement patterns and behaviour of adult males are largely unknown.

Sperm whales have a cosmopolitan distribution (Rice 1989), although particular areas are frequented more often than others and usually coincide with areas of high bottom topography, frontal systems and, associated with these, features areas of higher productivity (Berzin 1972; Waring *et al.* 1993; 2001; Jacquet and Whitehead 1996; Jacquet *et al.* 2000). The species is largely pelagic; females are rarely observed in waters of depths less than 1,000 m (Whitehead and Weilgart 2000) as are males, although in a number of specific areas males can be observed in waters less than 500 m (Whitehead *et al.* 1992; Jacquet *et al.* 2000; Waring *et al.* 2001). Females and immature individuals range large distances of at least 600x600 nautical miles throughout waters from the tropics to around 40-50°S (Rice 1989; Gaskin 1973). Males appear to have much larger ranges than females and move progressively into higher latitude waters with increasing

age, reaching waters close to the ice edge (Rice 1989). Seasonal migrations of mature males towards the more equatorial breeding grounds are thought to occur during winter months (Best 1979); although it is unclear whether particular migratory routes are taken and whether specific breeding grounds are frequented.

Movement patterns in this species appear to be largely dictated by foraging success and females have been estimated to travel in the order of 55 nautical miles per day in search of food (Jaquet *et al.* 2000). The sperm whale can be regarded as a dominant vertebrate predator of mesopelagic waters, with oceanic cephalopod species comprising the majority of its diet in most areas (Clarke 1980; Kawakami 1980). It is estimated that in the Southern Ocean alone, sperm whales consume in the order of 12 million tonnes of cephalopods per year (Clarke 1983; Rodhouse 1989). Adult females and immature animals have been tracked to depths of over 700 m (Lockyer 1977) and sub-adult and adult males have been tracked to over 1,000 m depth (Norris and Harvey 1972; Watkins *et al.* 1993, Wahlberg 2002). Dive duration has been observed to mostly be less than 45 minutes (Lockyer 1977; Papastavrou *et al.* 1989; Watkins *et al.* 1999; Wahlberg 2002) and foraging at depth occupies in the order of 75 % of a sperm whale's time (Whitehead and Weilgart 1991).

Sperm whales were exploited extensively by the whaling industry both during the open boat period of the 1700s and 1800s and later by modern whalers (Whitehead 2002) before protection afforded by the International Whaling Commission largely stopped the hunt for this species in the mid to late 1980s. Sperm whales were hunted in all major ocean basins and the records of this exploitation provide substantial records on the distribution of this species (Rice 1989). However, despite their extensive exploitation global population estimates are lacking both prior to and post-whaling. Statistics derived from catch-per-unit-effort have estimated that poluation numbers of sperm whales globally prior to whaling were in the order of three million and in the order of two million post-whaling. However, such estimates are subject to many biases (see Whitehead 2002 for a description of these) and are subsequently thought to be unreliable representations of population numbers. Recent analyses of mark-recapture, acoustic and visual censuses using scaling by primary productivity have reported an initial population estimate of 1,110,000 sperm whales globally with current population estimates only 32 % (360,000) of this initial figure (Whitehead 2002).

1.1.2. Research on sperm whales and its context in the Australian region

The pelagic and mostly underwater existence of sperm whales presents many difficulties for conducting live studies of this species, especially in areas where individuals do not regularly occur close to shore. Longitudinal studies have been undertaken on female groups and aggregations of immature males in areas where deep water occurs close to continental masses and island groups (*e.g.* Watkins *et al.* 1985; Gordon 1987; Whitehead 1990; Whitehead *et al.* 1992; Whitehead and Kahn 1992; Childerhouse *et al.* 1995; Jacquet *et al.* 2000) however, no similar areas have been identified in the Australian region to date.

Sperm whales were a large component of both shore-based and pelagic whaling operations in Australian waters since the early nineteenth century (Bannister 1974). American whalers concentrated on grounds offshore of Western Australia, predominantly in the colder months (Townsend 1935), which were later to become the basis for shore based whaling operations at Albany and Canarvon, Western Australia. Large catches of sperm whales were also taken off the coast of Tasmania and in the Tasman Sea by pelagic factories en-route to and from the Antarctic whaling grounds during the 1960s (Gaskin 1973; Bannister 1974). However, despite these concentrated whaling efforts and extensive efforts into collecting biological information from whale catches, little has been published on the life history of sperm whales in this region.

Sperm whales were recently classified as "Insufficiently Known" in the Australian region and priorities for research were identified in a Federal government initiated Action Plan for Cetaceans (Bannister *et al.* 1996). Key areas for research included the establishment of stock identity, distribution, abundance, basic biology and assessment of impacts associated with pollution, in an effort to provide baseline information on the status of this species in this area.

Information related to these research areas can be obtained from four sources:

1. Directed take;
2. Biopsy sampling;
3. Bycaught animals;
4. Stranded animals.

The directed take of animals is considered unethical and unnecessary by most biologists and environmental managers and this species has been protected under government law for close to two decades; biopsy samples are limited in their application to ecological questions and bycatch of this species is reported to be minimal or non-existent in Australian waters. Stranded, dead animals can however, provide a wealth of information and samples otherwise unable to be obtained. Mass strandings of this species in Tasmania are an infrequent but regular event, occurring approximately every five to ten years and present valuable opportunities to obtain information on this species in the Australian region.

1.2. AIMS OF THE PROJECT

The broad aim of this project was to examine the life history of complete or near complete female groups of sperm whales in an effort to contribute to the paucity of knowledge on two key areas of research identified for this species in the Australian Government's Action Plan on Australian Cetaceans: the basic biology and pollutant impacts on this species. This was undertaken by collecting, as comprehensively as possible, samples from three mass strandings of largely female groups of sperm whales that occurred on the west and north coasts of Tasmania in February 1998.

This study had the following specific objectives:

1. To determine the demographic characteristics of the three stranding groups by:
    - identifying the age structure of the three groups using refinements to contemporary age determination techniques;
    - calculate life tables and determine age-specific survival in females using established demographic models;
    - describe growth in females using established growth models.

2. To determine the characteristics of energy acquisition and the relationship between energy storage and life history strategies of this species by:
    - quantifying diet using hard part identification methods and interpreting differences between sex, age and stranding groups;
    - quantifying body fat condition via blubber thickness measurements and an analysis of blubber lipid content and interpreting these in light of mechanisms of energy storage and mobilisation.

3. To ascertain baseline data on organochlorine levels in this species and provide an ecological interpretation of concentrations and their distribution by:

- quantifying concentrations of organochlorines from blubber samples;
- interpreting those concentrations in light of dietary, blubber lipid content and demographic data;
- interpreting these data in light of what is known for other marine mammals in the Southern Hemisphere.

1.3. ORGANISATION OF THE THESIS

Because an investigation into the life history of a species involves a number of biological and ecological components, this thesis is comprised of five sections.

Section One (Chapters One and Two) provides a background to our current knowledge of the life history of this species and provides details of the three strandings in light of the stranding record of this species in Tasmania. Section Two (Chapters Three, Four and Five) examines issues associated with the techniques of age determination and the demographic characteristics of this species. Chapter Three details refinements to the current methodology associated with age determination in this species. Chapter Four examines the important issue of the precision of age determination in this species via a cross reading experiment. Chapter Five details the age structure of females involved in the three strandings, presents population parameters including survival and describes growth in females. Comparisons are made with population parameters and growth calculated from exploited populations. Section Three (Chapters Six and Seven) concerns energy acquisition and its interpretation in the life history strategy of this species. Chapter Six details the diet of sperm whales, differences in the diet according to age and sex and between stranding sites and discusses these in light of foraging strategies. Chapter Seven describes body fat condition and the use of blubber thickness measurements and blubber lipid content in establishing body fat condition. Results are interpreted in light of mechanisms for energy storage and mobilisation and in relation to the reproductive strategy of this species. Section Four (Chapter Eight) provides an ecological interpretation of concentrations of organochlorines in sperm whales and their distribution patterns between sexes, according to age and between strandings groups and places these results in the context of concentrations observed in sperm whales elsewhere. Section Five contains the general discussion (Chapter Nine) in which the life history components investigated are synthesized and described in light of the social structure of this species.

With the exception of the General Introduction (Chapter One) and the General Discussion (Chapter Nine), all chapters are self-contained and have been written as manuscripts for publication. As a result, there is some repetition of information between chapters, particularly concerning the description of methods used. Publications derived from or related to this thesis are detailed on a publications page. As collection of samples from the three mass strandings involved an extensive collaborative effort and aspects of this project involved collaboration with scientists from a number of other laboratories, a number of papers produced from this project are co-authored. I was senior author on all papers and organized field protocols, permits and equipment for the collection of samples, conducted all laboratory analysis or where samples could not be analysed by myself (*e.g.* identification and quantification of organochlorines in a registered and recognized laboratory) organized for their analysis. Margie Morrice and Deborah Thiele assisted with the collection and storage of samples from the three mass strandings. Kelly Robertson provided laboratory space, equipment and technical advice for the age determination studies and took part in the cross-reading experiment. Christina Lockyer and Dale Rice took part in the cross-reading experiment. Greg Hince conducted the final stages of the organochlorine analysis and provided technical advice on chemical analysis. As senior author on all papers, I have exercised my prerogative to recognize the contributions of my supervisors and included them as co-authors on papers where I see fit. With the exception of some minor formatting changes, papers have been presented as published. Abstracts and the literature cited for each paper have been removed and incorporated into the general abstract and reference list for consistency.

CHAPTER TWO

AN INTRODUCTION TO THREE MASS STRANDINGS OF SPERM WHALES, *Physeter macrocephalus*, IN SOUTHERN AUSTRALIAN WATERS[1].

2.1. INTRODUCTION

Sperm whales (*Physeter macrocephalus*) occur frequently in stranding records worldwide (Robson and van Bree 1971; Rice *et al.* 1986; Christensen 1990; Gallagher 1991; Evans 1997). In the south-east Australian region of Tasmania, sperm whales are frequent stranders. Sixty nine stranding events involving 375 individuals have been documented along the Tasmanian coastline since 1911 (Guiler 1978; McManus *et al.* 1984; Nicol 1987; Warneke 1997). Of these, 16 events (involving a total of 321 whales) can be termed mass strandings, *i.e.* those involving two or more individuals (other than mother-calf pairs).

This chapter describes the three most recent mass strandings of sperm whales in Tasmania, all of which occurred on the west and northwest coasts in February 1998 (Figure 2.1). Three mass strandings of this species in such close temporal proximity have not been reported in this area before, and this is the first time that data have been comprehensively collected from complete or near-complete groups of sperm whales from Tasmanian waters.

Most information on the general biology of sperm whales has been derived from single stranding events, whaling operations and samples collected from animals under special permit (Best 1968, 1970; Berzin 1972; Lockyer 1991; Richard *et al.* 1996). The information derived from these three mass strandings is important for a number of reasons. Firstly, animals involved in single stranding events are often compromised to some extent by disease or age (Aguilar and Borrell 1994b), and therefore provide biased information on the free-ranging biology and ecology of cetaceans. Mass strandings on

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the other hand, are thought to be composed largely of individuals representing healthy, free-ranging populations and provide information on a cross-section of that population (St. Aubin and Geraci 1979). Secondly, to date, data that have been published from groups of sperm whales are frequently based on only a sub-sample of each group. This is either because only part of any live group of animals can be sampled from or collected at the one time due to the behaviour of these groups, or because of logistical restrictions at mass stranding events. We were able, in most instances, to collect samples from all individuals involved in the strandings. Thirdly, information on the life history of sperm whales in this region is sparse. These three strandings provided a unique opportunity to enhance our understanding of the demographics, reproductive condition, diet, health, genetic and social structure of this species in southern Australian waters.

This chapter provides a general description of the strandings, the behaviour of the animals during the stranding, detailed information on the sex, age, size, reproductive condition, general condition and diet of the animals involved and the context of this stranding in relation to the historical Tasmanian stranding record for this species.

2.2. MATERIALS AND METHODS

2.2.1. Ocean Beach, Strahan (Stranding 1)

On the evening of 3 February 1998, several sperm whales were reported ashore on Ocean Beach near Strahan (42°18'S, 145°16'E). By the morning of 4 February, 66 animals had stranded, 12 of which were still alive. A rescue operation towed two animals (one male, one of unknown gender) offshore by midday, at which time two females and two males remained alive. By 0700 of 5 February only one female and one male were alive. The female was euthanased and the male was refloated and towed offshore at 1630.

2.2.2. Greens Pt. Beach, Marrawah (Stranding 2)

At 0700 on 19 February 1998, local residents reported a group of sperm whales in a tightly grouped formation off Greens Pt. Beach, Marrawah (40°55'S, 144°39'E). Shortly after 1000 they began to strand. By 0700 of 20 February only five of the 35 whales ashore were alive, with rough seas inhibiting any chance of rescue. At 1300 one male and one female were alive. By 0900 on 21 February the female had died and at 1100 the male was euthanased.

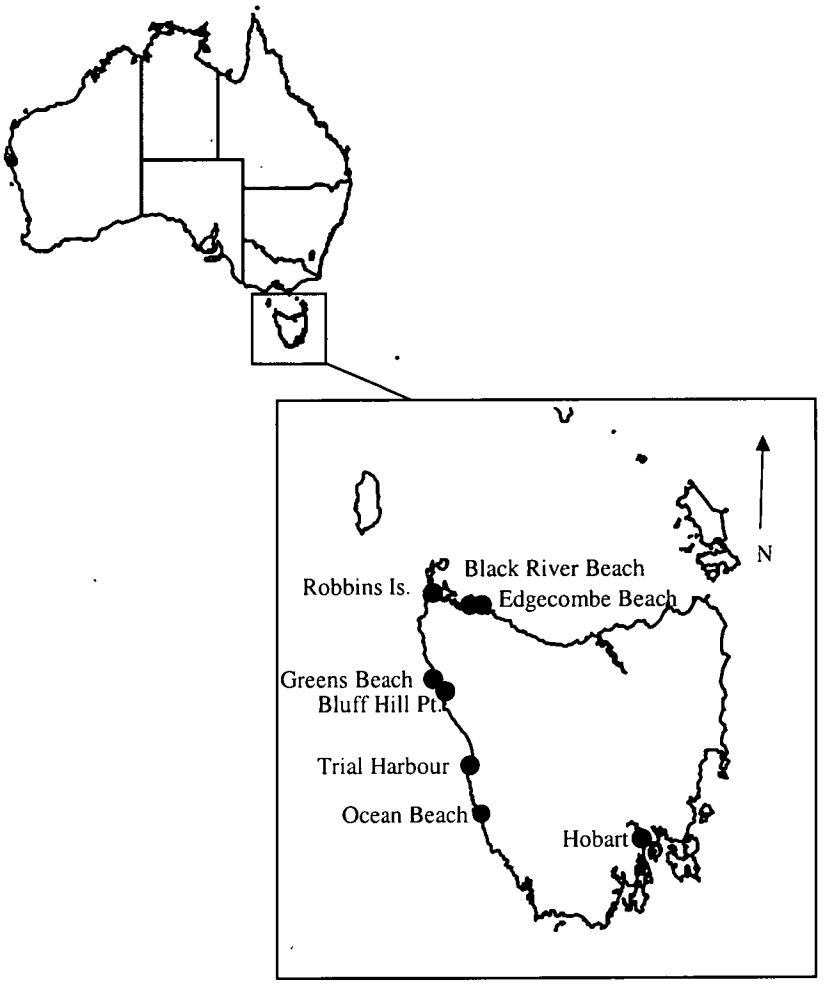


Figure 2.1: Location of sperm whale strandings, Tasmania, Australia 1998.

2.2.3. Black River Beach, Stanley (Stranding 3)

At 1000 on 28 February 1998, 11 sperm whales were reported ashore at Black River Beach, Stanley (40°50'S, 145°17'E). At 1230 ten females were found deceased and one male alive. The male sperm whale was towed offshore at 0400 on 1 March, but later re-stranded at Edgecumbe Beach (40°52'S, 145°25'E), ten kilometres east at 1600. This animal was positively identified from Black River Beach by the presence of a lower jaw deformity. At 0230 on 2 March the whale was towed offshore again and was followed for approximately 14 kilometres, after which it was observed to swim away.

2.2.4. Sample Collection

The behaviour of whales prior to, during and after each stranding was documented. Biological samples were collected from whales post mortem 48 hours after the stranding was reported at Ocean Beach (STR1) and 24 hours after reporting at Greens Pt. Beach (STR2) and Black River Beach (STR3; Table 2.1). Sampling procedures were similar at all three strandings and were based on protocols following Geraci and Lounsbury (1993).

All whales were numbered sequentially along each beach. At STR1 and STR2, this was conducted after animals had been moved up the beach and out of the surf zone, so the numbering system does not reflect the original position of animals along the beach. At STR3, numbering was carried out from east to west and does reflect the original position of animals along the beach. Sex, total length [tip of upper jaw to deepest notch in fluke taken in a straight line dorsally (Norris 1961)]; ventral total length (tip of lower jaw to deepest notch in fluke taken ventrally in a straight line) and fluke span (distance from tip to tip) were recorded. Photographs of the head region, flukes and genital region were taken to document pigmentation patterns and scarring, and to verify the sex of all animals at STR2 and STR3.

Mammary glands and reproductive organs could not be collected because of rapid decomposition. Lactation status was determined by applying pressure to teats and through the identification of the presence of milk via dissecting mammary glands.

Blubber thickness was measured and a sample of blubber taken from a position approximately half way along the dorsal surface of each animal (the distance of this site from the tip of the upper jaw was measured for ten animals at STR1, STR2 and STR3). Blubber was wrapped in foil and frozen. Skin and muscle samples were also collected from this site: the skin was preserved in dimethylsulfoxide (DMSO) and frozen and the muscle was frozen.

For those animals that were sampled for stomach contents, each stomach was emptied of all contents, or as much of the contents were collected as was possible. In all cases the extent of sampling was documented. Stomach samples were only available from STR1 and STR2.

A mid-section of the lower jaw was collected from animals at STR1 and near-complete lower jaws were collected from animals at STR2 and STR3. Cleaned teeth used to determine the age of individuals. Teeth were prepared for age determination using the methods detailed in Chapter Three. Ages were determined from the identification and counting of growth layer groups (GLGs) in the dentine of sectioned teeth as detailed in Chapter Four. Growth layer groups were interpreted as those identified in the sperm whale section of the report from the Workshop on Age Determination of Cetaceans and Sirenians (Perrin and Myrick 1980). For those specimens in which the neonatal line could be identified (many of the teeth had worn tips and therefore were missing the enamel, neonatal line and the first few growth layer groups), this was not included in the total number of GLGs. The presence of erupted maxillary teeth for those animals at STR2 and STR3 was noted. Visible parasites, deformities and scarring were noted, although time and operational restrictions prevented an extensive investigation into the presence of parasites.

For analytical purposes, females were assumed to be sexually mature at lengths greater than 850 cm and ages greater than 13 years and males at lengths greater than 1,200 cm and ages greater than 19 years (Best 1968; Lockyer 1981b; Rice 1989).

2.3. RESULTS

2.3.1. Behaviour

The stranding at STR2 was the only stranding at which the behaviour of whales was documented prior to and throughout the stranding. However, approximately 30 additional whales were observed offshore at the time of the STR1 stranding. These animals did not strand and were not seen again. It is not clear whether these animals were part of a larger group including those animals that stranded, or were part of a separate group.

Table 2.1: Type and numbers of data and samples collected at the three mass strandings, Tasmania 1998.

Sample/Data collected	STR1	STR2	STR3
Total stranded	66	35	11
Morphometrics			
Total dorsal length	63	35	11
Total ventral length	10	35	10
Fluke span	10	–	10
Blubber thickness	57	35	10
Samples			
Skin	63	37[#]	11[#]
Blubber	63	35	11[#]
Muscle	53	35	11[#]
Stomach contents	14	21	–
Teeth	58	26	10

[#]includes foetal samples

Just prior to the stranding at STR2, a tightly packed and what appeared to be united group of whales, were observed to move from an area offshore, in towards the surf zone. One animal separated itself from the group and moved in a direction parallel with the shore. Disparate reports on the size and sex of this animal prevent an accurate identification. Its swimming action was described as frantic – it swam in a zigzag fashion, churning up the water as it progressively moved inshore until it stranded on the beach. The remaining animals followed this whale in groups of two to three until they were inside the surf zone, after which they seemingly were passively pushed inshore by the wave action of the beach. The last two whales to strand however showed a different pattern in moving inshore. These were observed to swim along the shoreline, parallel with the beach in a northward direction. They then turned south, swimming back past all the other stranded whales and then turned inshore and appeared to actively strand together at a site further south along the beach, separate from the main group of animals.

2.3.2. Additional stranded whales

Three additional sperm whales were discovered along the west Tasmanian coastline during February 1998. A 7.7 m male was discovered offshore of Trial Harbour (41°55.7'S, 145°10.3'E), 25 kilometres north of Ocean Beach on 8 February with rope burns around its tailstock. A 9.2 m sperm whale of unknown gender was sighted by air at Bird Point, Robbins Island (40°39'S, 144°55'E), over 200 kilometres north of Ocean Beach on 3 February, but was not reported until 23 February – the animal was severely decomposed when investigated on 24 February. A 5.0 m sperm whale of unknown gender was discovered on Bluff Hill Point (41°00.5'S, 144°36.5'E), 1.5 kilometres south of Greens Beach on 26 February. This animal was severely decomposed and was missing its tail. Because it is not possible to associate any of these whales to any of the three strandings, those data collected from these animals have not been included in the analyses presented here.

2.3.3. Sex Ratios

Females dominated all three stranding groups (Table 2.2). Of these, the majority (STR1: 95.2 %; STR2: 96.0 %; STR3: 100 %) were mature.

Only 15 (12.9 %) of the 115 whales involved in the strandings were males, ten of which were involved in STR2. All males were less than 12 m, so therefore all three groups were composed of mature females and juveniles and calves of both sexes. None of the rescued males were measured; however, all were described as medium sized, suggesting that they were of a similar size to those that were sampled.

Table 2.2: Percentage of female sperm whales in stranding and free-ranging groups.

Group	Location	Type of group	Number of animals	Percentage female	Reference
STR1	Tasmania, Australia	stranding	64	96.9	this paper
STR2	Tasmania, Australia	stranding	35	71.4	this paper
STR3	Tasmania, Australia	stranding	11	90.9	this paper
O#A	Japan	free-ranging	19	84.2	Ohsumi (1971)
O#B	S. Indian Ocean	free-ranging	12	83.3	Ohsumi (1971)
O#C	S. Indian Ocean	free-ranging	39	71.8	Ohsumi (1971)
R	Oregon, USA	stranding	41	68.3	Rice *et al.* (1986)
SR#10	Tasmania, Australia	stranding	14	78.6	McManus *et al.* (1984)
SR#11	Tasmania, Australia	stranding	9	55.6	McManus *et al.* (1984)
SR#13	Tasmania, Australia	stranding	16	100.0	this paper[1]

[1]personal communication, R. Warneke.

2.3.4. Morphometric measurements

The three stranding groups were dominated by animals 1,050.0-1,150.0 cm in length (Table 2.3, Figure 2.2). There were no significant differences between the total lengths of whales in the three strandings groups (ANOVA, $F_{2, 106}=0.7$, $P=0.5$). This was also the case for females (ANOVA, $F_{2, 94}=0.4$, $P=0.6$) and when all immature animals were excluded (therefore comparing mature females) from the dataset (ANOVA, $F_{2, 90}=1.2$, $P=0.3$). Total length was significantly positively related to the number of GLGs (Regression; all: $r^2=0.3$, $F_{1, 90}=40.0$, $P<0.001$; females: $r^2=0.7$, $F_{1, 82}=31.3$, $P<0.001$; males: $r^2=0.9$, $F_{1, 6}=174.0$, $P<0.001$). Calculated Gompertz growth curves (see Chapter Five for further details) for females and males (Figure 2.2) resulted in the following equations:

$$\text{Females: } L_{(t)}=1080.67\exp\{1.03[1-\exp(-0.18t)]\},\ r^2=0.8.$$
$$\text{Males: } L_{(t)}=554.75\exp\{0.68[1-\exp(-0.15t)]\},\ r^2=0.9.$$

Both ventral total length (means for each stranding: STR1: 908.4±304.4 cm, n=10; STR2: 1,038.7±46.2 cm, n=35; STR3: 1,045.1±33.3 m, n=10) and fluke span (means for each stranding: STR1: 287.1±98.0 cm, n=10; STR2: 551.8±56.7 cm, n=35; STR3: 316.7±14.2 m, n=10) as expected, were positively related to dorsal total length (Regression; ventral length: $r^2=0.95$, $F_{1, 53}=1,113.3$, $P<0.001$; fluke span: $r^2=0.3$, $F_{1, 17}=7.5$, $P=0.01$; Figure 2.5). Ventral length was positively related to age (Regression; $r^2=0.2$, $F_{1, 40}=10.3$, $P=0.003$), while fluke span was not significantly related to age (Regression; $r^2<0.001$, $F_{1, 11}=0.7$, $P=0.4$). Determination of the relationships between dorsal total length, age and fluke span could only be carried out on data from females as no fluke measurements were taken from males.

2.3.4. Age structure

The number of GLGs identified in the teeth of individuals from the three stranding groups ranged from 0.75-64 (Table 2.4, Figure 2.3). These age estimates are minimums as most teeth were worn at the tips, therefore missing the enamel, neonatal line and the first few GLGs. STR3 differed from the other two strandings in that it contained no juveniles; this group contained the highest mean number of GLGs. Age estimates between the three stranding groups were not significantly different (ANOVA, $F_{2, 89}=1.5$, $P=0.2$). Age estimates of males were significantly lower (t-test, $t_7=3.8$, $P<0.001$) than that of females (Table 2.4).

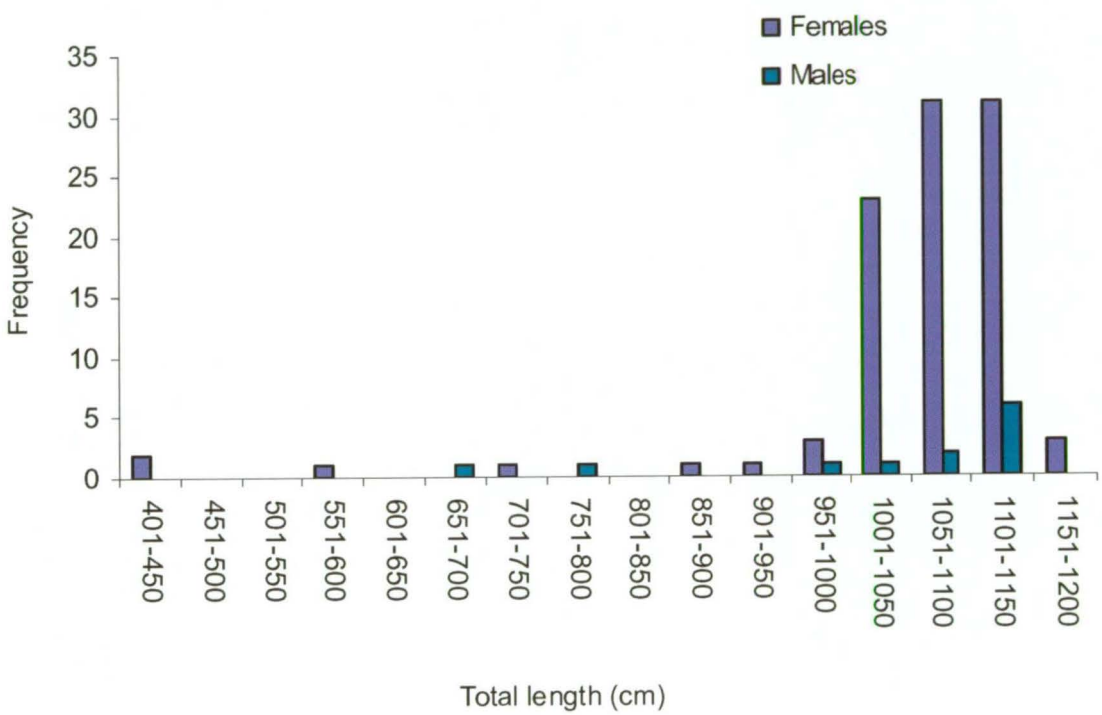


Figure 2.2: Distribution of the total lengths of southern Australian sperm whales.

Table 2.3: Total lengths (cm) of sperm whales in stranding and free-ranging groups. Number of animals in parentheses.

		STR1	STR2	STR3	O#A^	O#B^	O#C^	R*
All	Mean±S.D	1,045.8±144.2 (63)	1,069.4±42.4 (35)	1,091.9±30.4 (11)	956.3±75.4 (19)	933.3±71.9 (12)	887.5±126.8 (39)	1,053.7±53.2 (41)
	Range	417.0-1,200.0	575.0-1,150.0	1,044.0-1140.0	850.0-1,111.0	780.0-1,010.0	540.0-1,080.0	930.0-1,150.0
Immature E	Mean±SD	521.7±171.9 (3)	575.0 (1)	–	–	790.0±14.1 (2)	820 (1)	–
	Range	417.0-720.0				780.0, 800.0		
Mature E	Mean±SD	1,078.9±58.4 (59)	1,063.1±38.4 (24)	1,089.1±30.4 (10)	970.6±72.0 (16)	967.5±27.7 (8)	956.7±56.0 (27)	1,048.6±48.8 (28)
	Range	890.0-1,200.0	980.0-1,150.0	1,030.0-1103.0	860.0-1,110.0	920.0-1,010.0	850.0-1,080.0	930.0-1,140.0
Immature Γ	Mean±SD	667 (1)	1,055.5±107.7 (10)	1,120.0 (1)	880.0±43.6 (3)	940.0±28.3 (2)	730.9±11.6 (11)	106.3±61.7 (13)
	Range		780.0-1,150.0		850.0-930.0	920.0, 960.0	540.0-900.0	930.0-1,150.0

^: Ohsumi (1971), free-ranging groups.
*: Rice *et al.* (1986), stranding group.

2.3.6. Reproductive Condition

Of 93 adult females examined, lactation state was determined for 38. Of these females, four (10.5 %) were lactating and 34 were resting. The stranding group at STR1 contained one lactating female (7.1 %, n=14), STR2 contained two (11.8 %, n=17) and one lactating female was identified at STR3 (14.3 %, n=7). Age estimates of lactating females ranged from 24-64 years.

Two foetuses were aborted from females at STR1, four at STR2 and one at STR3. Minimum pregnancy rates derived from fetus numbers at each of the strandings were 3.4 % (two of 59 mature females) at STR1, 16.7 % (four of 24 mature females) at STR2, 10.0 % (one of 10 mature females) at STR3 and overall 7.5 % (seven of 93 mature females). Age estimates of pregnant females ranged from 25-52 years. These figures are minimums, as extensive investigation of the reproductive tracts of females to identify non-aborted fetuses was not carried out. Total lengths of four of these fetuses were 50, 280, 340 and 370 cm.

2.3.7. Scarring

Teeth rake marks were common on the stranded animals, especially around the head and on the tail flukes (Figure 2.6). Of those animals photographed at STR2 (n=28) and STR3 (n=10), 63 % (n=24) were identified as having such scars present. Tooth rakes were present in two forms (1) large and widely spaced, probably either the result of orca (*Orcinus orca*) attacks or other sperm whales and (2) small and less widely spaced, possibly from sharks. Scars, most likely derived from squid sucker hooks (Figure 2.6), were present on the head region of 66 % of animals (n=25), and individual, white, star-shaped scars (Figure 2.6) occurred on 76 % (n=29). Fresh bites from cookie cutter sharks (*Isistius brasiliensis*) were also present. Tail flukes had holes or scalloped shaped pieces (Figure 2.6) missing from the trailing edges in 89 % of all animals (n=34). The youngest animal with tooth rakes was estimated to be 1.5 yr, the youngest with sucker scars and fluke holes/scallops was estimated to be five years and the youngest with star-shaped scars was estimated to be 19 years. When the incidence of these four forms of scarring were log-regressed with length and age, only star-shaped scars were found to be significantly related to total length (Log model: $2*[LL(N)-LL(0)]=5.2$, d.f.=1, $P=0.02$).

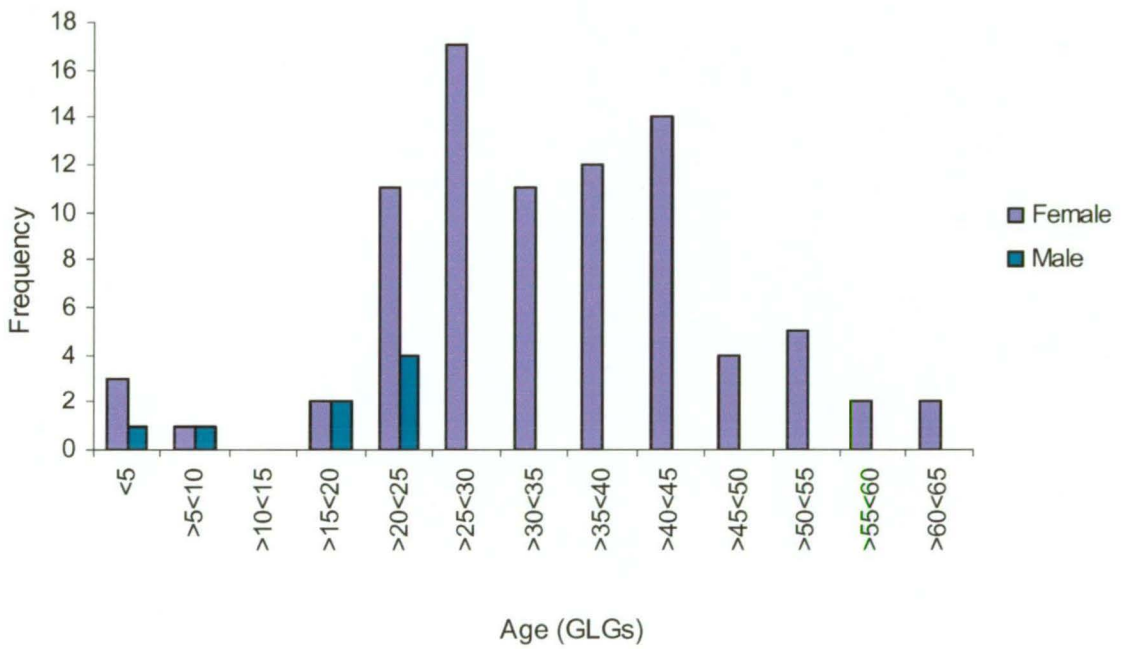


Figure 2.3: Distribution of the ages of southern Australian sperm whales.

Table 2.3: Ages (number of GLGs) of sperm whales in stranding and free-ranging groups. Number of animals in parentheses.

		STR1	STR2	STR3	O#A^	O#B^	O#C^	R*
All	Mean±SD	31.5±11.8 (56)	33.5±15.3 (29)	40.3±13.8 (7)	13.8±9.8 (19)	16.1±9.1 (12)	14.7±10.9 (39)	22.9±10.8 (41)
	Range	0.75-53.0	1.5-64.0	22.0-61.0	3.0-41.0	4.0-35.0	0.0-45.0	11.0-58.0
Immature females	Mean±SD	2.8±3.6 (3)	1.5 (1)	–	–	5.0±1.4 (2)	5.0 (1)	–
	Range	0.75-7.0				4.0, 6.0		
Mature females	Mean±SD	33.7±9.0 (52)	39.9±12.2 (21)	40.3±13.8 (7)	15.4±9.8 (16)	20.4±7.9 (8)	19.1±10.1 (27)	25.3±12.4 (28)
	Range	17.0-53.0	24.0-64.0	22.0-61.0	6.0-41.0	12.0-35.0	1.0-45.0	11.0-58.0
Immature males	Mean±SD	1.9 (1)	19.3±6.6 (7)	–	5.0±2.6 (3)	10.0±0.0 (2)	4.8±3.4 (11)	17.8±2.2 (13)
	Range		5.0-24.0		3.0-8.0	10.0, 10.0	0.0-9.0	14.0-21.0

^: Ohsumi (1971), free-ranging groups.
*: Rice *et al.* (1986), stranding group.

2.3.8. Maxillary Teeth

Of the 35 animals at STR2, nine (25.7 %) were noted to have teeth that had erupted through the maxillary gumline. At STR3, two (20.0 %, n=10) whales were documented to have erupted maxillary teeth. Total numbers of erupted maxillary teeth per animal ranged from one to eleven (Table 2.5). Erupted maxillary teeth occurred only in adult animals, however, the numbers present were not correlated with length (all animals pooled, Pearson correlation coefficient=0.1, d.f.=1, P=0.7), or with estimated age (all animals pooled, Pearson correlation coefficient=0.2, d.f.=1, P=0.3). The youngest animal with erupted maxillary teeth was estimated to be 23 years.

Table 2.5: Number of maxillary teeth, length (cm) and age estimates (number of GLGs) in sperm whales from STR2 and STR3.

STR2			STR3		
Length	Age	Maxillary teeth	Length	Age	Maxillary teeth
1100	27	1	1082	50	1
1110	58	1	1102	–	11
1060	49	4			
1020	45	3			
1060	38	1			
1040	43	4			
1150	23	4			
1020	–	8			
1105	–	1			

2.4. DISCUSSION

Sperm whales are one of the most commonly stranded cetacean species on the Tasmanian coastline (Guiler 1978; McManus et *al.* 1984; Nicol 1987; Warneke 1997). The majority of sperm whales reported in the stranding record are from mass stranding incidents (85.6 %) and these three recent strandings have contributed 30.7 % of the total number of sperm whales reported on Tasmanian shores to date since 1911. Mass stranding events have commonly involved numbers of animals larger than 20, but range in number from two to 58 (Table 2.7). Thirteen of the 16 (81.0 %) mass stranding events have occurred on the northwest and west coasts of Tasmania, suggesting this coastline is particularly prone to sperm whale strandings.

2.4.1. Sex Ratios

Studies into the social structure and organisation of female sperm whales suggest that these animals form socially cohesive groups of ten to 30 adult females and immature individuals based on mixed matrilines and long term associations (Whitehead *et al.* 1991; Mesnick *et al.* 2003). These groups are themselves composed of mostly permanent units of 12 to 13 individuals (Whitehead *et al.* 1991; Richard *et al.* 1996). It is thought that these units merge and separate from others, forming temporary associations that in turn, merge and separate to form temporary larger aggregations for periods of time (Whitehead and Kahn 1992). STR1 and STR2 may indeed be composed of several of these units which have merged to form the larger aggregations that stranded. Preliminary genetic studies of these three female groups of sperm whales support the presence of both 'kith' (close, but not genetically related companions) and 'kin' in these groups (Mesnick *et al.* 2003). These results suggest that individuals from each of the stranding groups were observed to comprise both close relatives and individuals that were not closely related to others. Further investigations into the genetic structure of these groups will provide greater insight into the social structure and relationships of animals within these groups.

At other strandings and in free-ranging groups (Ohsumi 1971; McManus *et al.* 1984; Rice *et al.* 1986) percentages of females vary from 55-100 %. Mature females dominate all groups: when immature animals are excluded mature females comprise 100 % of the groups. Groups of sperm whales have been described as containing approximately 78 % Best (1979), 67-89 % Richard *et al.* (1996) and anywhere between 36-100 % (Rice 1989) females. Such percentages are similar to the composition of the three stranding groups here, as well as the stranding group in Rice *et al.*, (1986), the free-ranging groups in Ohsumi (1971) and past sperm whale strandings from Tasmania. It appears that a large proportion of sperm whales in Tasmanian stranding record comprise female groups.

2.4.2. Morphometric measurements and age structure

All three strandings were composed of similar sized animals. Average total lengths of animals from the Tasmanian strandings were significantly different from those of other free-ranging (Ohsumi 1971) and stranding (Rice 1986) groups (ANOVA, $F_{6, 213}=13.5$, $P<0.001$). This was also the case when all immature animals were excluded from the dataset (ANOVA, $F_{6, 175}=26.8$, $P<0.001$). A Tukey pairwise comparison was conducted on the two datasets (all animals and all mature animals) and revealed that the stranding groups (both Australian and North American) were composed of significantly larger animals than the free-ranging groups. There were no significant differences between the

Australian and North American stranding groups (ANOVA, $F_{3, 146}$=0.6, P=0.6).

Those groups presented in Ohsumi (1971) were only a part of the original groups identified (A: 73 %; B: 30 %; C: 81 %). It may be that larger members of these groups are missing from the sample, therefore biasing the groups with smaller animals. It is also possible that whales from different geographic regions and genetic stocks differ in general morphology, including total length. This has been postulated elsewhere for other groups of sperm whales (Arnbom and Whitehead 1989; Waters and Whitehead 1990). Temporal differences in sampling may also account for variations in the composition of groups encountered and so therefore, in the average length of animals documented. If female sperm whale groups merge and separate over periods of time, this will result in changes in the composition of groups and consequently, a change in the size structure of animals in these groups both temporally and geographically.

Table 2.7: Numbers and sex ratios of sperm whales involved in mass strandings in Tasmania 1911-1998.

Date	N	Sex	Location region	Reference
February 10, 1911	37	36M:1F	NW	Guiler (1978)
February 18?, 1953	2	2M	NE	this paper[1]
September 22, 1970	58	11M:41F:6?	NW	Guiler (1978)
March 28, 1971	32	–	NW	Guiler (1978)
January?, 1975	3	–	NE	Nicol (1987)
October 4, 1975	2	2F	NW	Guiler (1978)
March 7, 1980	3	–	W	McManus *et al.* (1984)
January 15, 1981	26	3M:7F:16?	W	McManus *et al.* (1984)
September 25, 1981	2	2M	NE	McManus *et al.* (1984)
January 26, 1982	14	3M:11F	W	McManus *et al.* (1984)
February 9, 1982	9	4M:5F	NW	McManus *et al.* (1984)
January 14, 1989	5	–	W	this paper[1]
October 8, 1989	16	16F	NW	this paper[1]
February 3, 1998	66	2M:62F:2?	W	this paper
February 26, 1998	35	10M:25F	NW	this paper
February 28, 1998	11	1M:10F	NW	this paper

[1]personal communication, R. Warneke.

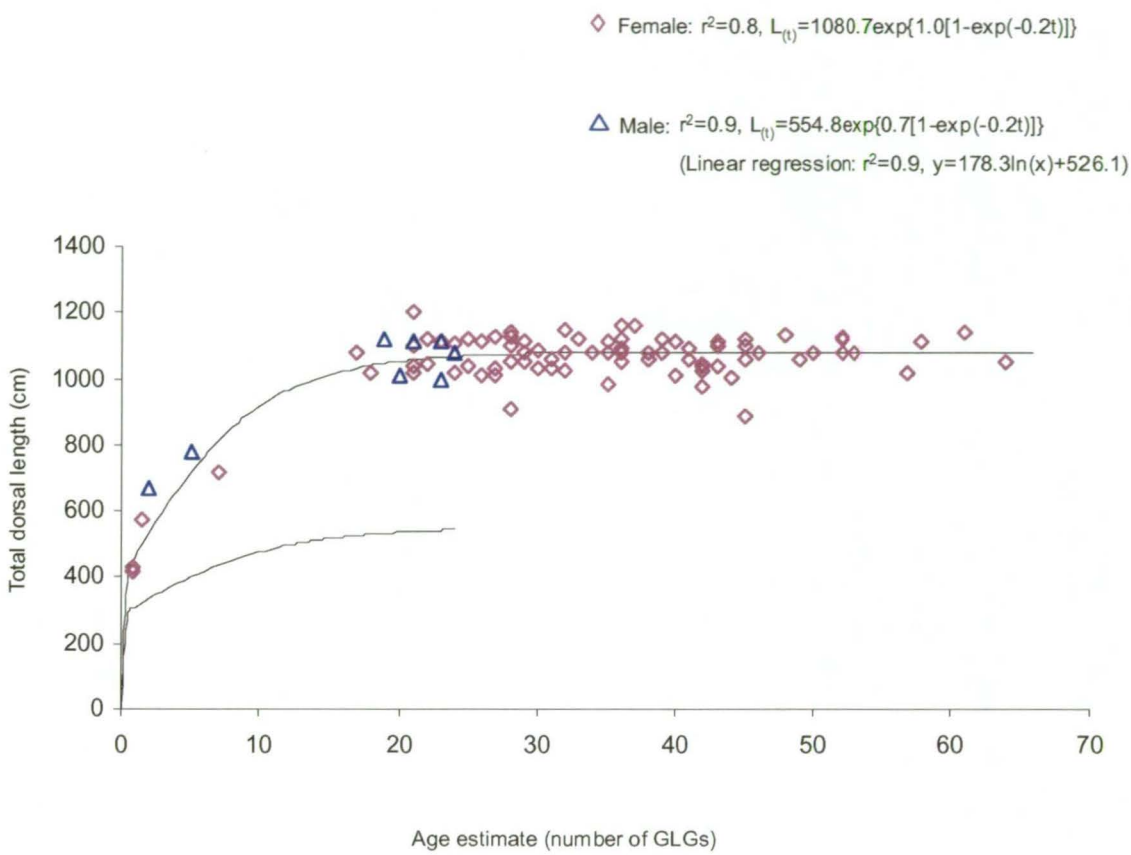


Figure 2.4: The relationship between total length (cm) and age (number of GLGs) in southern Australian sperm whales.

The Australian stranding groups and those in Rice *et al.* (1986) also contained larger numbers of older females in comparison to the free-ranging groups. The average age estimated for adult females in the three Tasmanian groups (STR1: 33.7±9.0 years; STR2: 39.9±12.2 years; STR3: 40.3±13.8 years) and in the North American group (25.3±12.4 years) are higher than those females in the three free-ranging groups (A: 17.3±10.7 years; B: 20.4±7.9 years; C: 19.6±9.5 years) detailed in Ohsumi (1971). It is thought that physical maturity and an attainment of maximum total length in females is not reached until at least 30 years (Lockyer 1981b) and if so, many of the females in the free-ranging groups may not have yet reached their maximum total length.

Past whaling operations may have skewed the age distribution of sperm whale populations through the targeting of larger (and potentially older) animals. It may be that those populations sampled in Ohsumi (1971) during exploitation contained a deficit of larger adult females. The cessation of whaling operations and the subsequent decrease in mortality rates may have resulted over time in a moderation of such a deficit. This would result in an increase in the proportions of larger and older animals within current populations and the occurrence of groups such as those stranding groups documented here.

Both Gompertz growth equations demonstrated high r^2 values (Females: r^2=0.8; Males: r^2=0.9). However, the growth curve calculated for females was observed to fit those data from the three strandings more closely than that calculated from male values. This disparity reflects the lack of larger males in the strandings groups. As a result, the equation calculated from a linear regression of total dorsal length against age in males provided a closer fit to the data ($y=178.3\ln(x)+526.1$) than the equation derived from the Gompertz growth curve. The majority of previously published growth curves for sperm whales have been fitted to age-length data by eye rather than through the calculation of growth curves (Nishiwaki, Ohsumi &Maeda, 1963; Best, 1970; Gambell, 1972; Lockyer, 1981). The growth curve presented here documents growth in female sperm whales from the south-eastern Australian region for the first time and provides the basis for comparisons with populations of female sperm whales elsewhere.

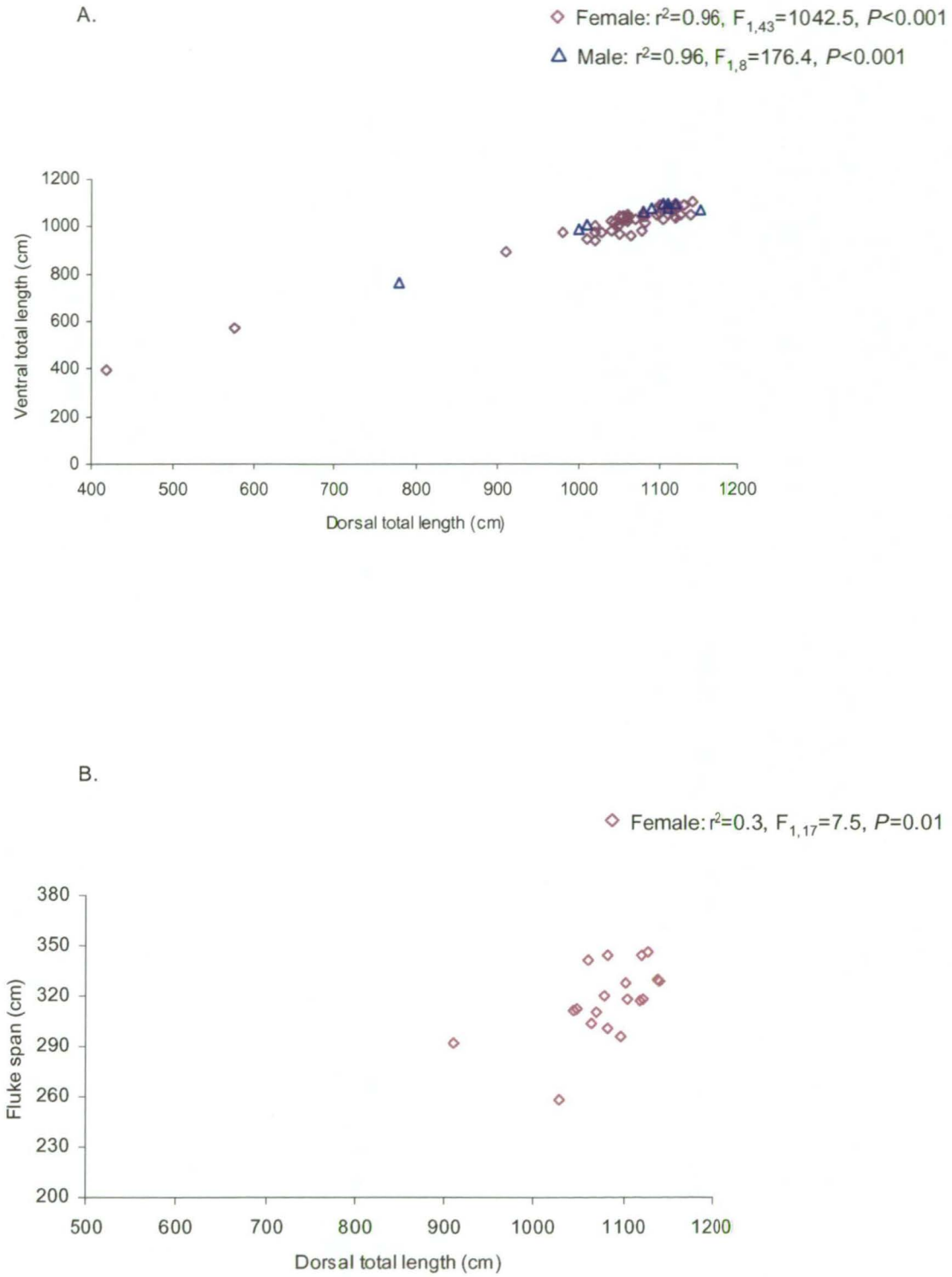


Figure 2.5: Relationships between dorsal total length and (a) ventral total length and (b) fluke span in southern Australian sperm whales.

Determining the relationship between dorsal total length and other morphometric measurements such as ventral total length and fluke span is useful in two respects. They document growth in these morphometric values for animals in Australian southern waters and they provide useful equations for the calculation of dorsal total length when such a measurement cannot be taken, but other morphometric measurements are. While the relationship between dorsal and ventral total length was described closely by the equation determined in this study (r^2=0.96), the equation calculated from the relationship between fluke span and total dorsal length did not fit the data closely (r^2=0.3). As a result, measurements of fluke span cannot be regarded to effectively predict total dorsal length. Care must also be taken in using these equations for predicting variables. Both Harrison Matthews (1938) and Clarke and Paliza (1972) observed that animals from different areas differed in their morphology. Consequently, these equations may not be suitable for sperm whales sampled in other geographic regions.

The time at which juvenile males are thought to disperse from their parental groups varies throughout the literature. Richard *et al.* (1996) proposed that males dispersed between the ages of 2.7-10.9 years, while Rice (1989) suggested dispersal occurred between the ages of 15.0-21.0 years. The presence of juvenile males with a maximum age estimate of 24 years in the Tasmanian groups is somewhat disparate from this and poses some interesting questions. Two obvious questions can be asked: (1) do juvenile males disperse at older ages in sperm whale groups from this region? (2) do juvenile males form associations with female groups after dispersal from their parental groups? Genetic studies of these three groups may provide insight into the relationships of these older juveniles with the other animals in their stranding groups.

2.4.3. Reproductive Condition

Of the 38 females in which lactating condition was positively confirmed, only four were lactating. Of those calves identified as having milk present in their stomachs, all were less than 720 cm. If we assume that all animals less than 720 cm were suckling and therefore had mothers that were lactating, four females at STR1 should have been lactating, one at STR2 and none at STR3. If we include the late-term foetuses aborted, these numbers become four at STR1 (6.8 % of mature females), three at STR2 (12.5 %) and one at STR3 (10.0 %). These numbers are minimums, as females were not examined for fetuses. Other free-ranging (Ohsumi 1971) and stranding (Rice *et al.* 1986) groups contained variable percentages of lactating females ranging from 0-51.9 %. Percentages of lactating females calculated from whaling operations are also variable: 16 % in whales caught in Western Australia during 1964-65 (Best *et al.* 1984) and 37.5 % in South Africa

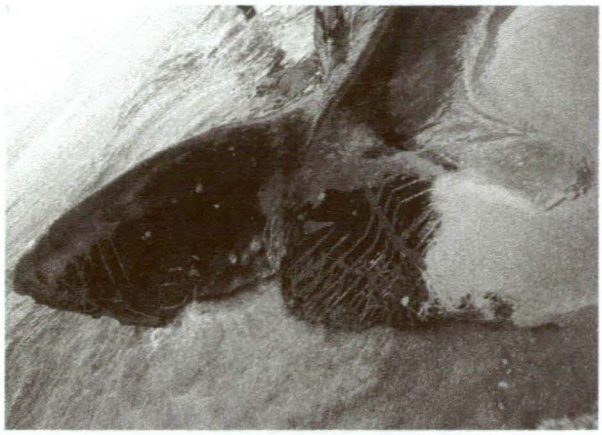
during the period 1962-67 (Best *et al.* 1984). These percentages suggest that proportions of lactating females may be highly variable throughout groups of sperm whales. Part of this variability, however, may be due to the underestimation of the identification of lactating females when only visual inspection is used. If so, lactating females can only be accurately quantified by dissection and histological inspection of the mammary glands.

Foetal lengths (50-370 cm) were similar to those documented from South Africa [25-420 cm during the month of March (Best 1968)], suggesting similar reproductive cycles characterized by asynchronous conception and an overlap in a gestation period of greater than twelve months. The smaller foetuses comprise the current year's cohort, the larger foetuses comprise the previous year's cohort. Foetuses identified in other stranding (Rice *et al.* 1986) and free-ranging (Ohsumi 1971) groups sampled during the breeding season ranged from 264 to 462 cm. Such groups appeared to have only contained foetuses conceived from the previous season. This absence may be a factor of incomplete sampling and therefore, undocumented foetuses in these groups.

Length of gestation varies throughout the literature, from 14 to 15 months (Best 1968; Rice 1989), 15-16 months (Best *et al.* 1984) and 14.5-16.5 months (Lockyer 1981b). If we assume that foetal growth rates are similar between Australian and South African sperm whales, and that length at birth is approximately 400 cm (Best 1968; Lockyer 1981b), when the four foetal lengths documented here are plotted against data from Best (1968), conception dates range from October to March and calving dates range from December to April.

Weaning is thought to take place in a calf's second year at about 670 cm (Best 1968; Lockyer 1981b), although opportunistic suckling may continue for much longer than this (Best et *al.* 1984). Three immature females (417, 575 and 720 cm) were found to have milk present in their stomachs, the largest also containing cephalopod beaks, suggesting that weaning may occur at a similar length and age to those published previously.

A.



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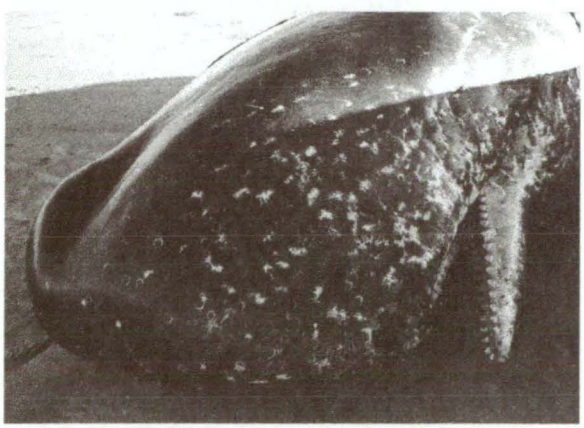


Figure 2.6: Scarring in Tasmanian sperm whales: (a) tooth rakes and fluke marks; (b) squid sucker hook scars; (c) star-shaped scars possibly from *Isistius brasiliensis*.

2.4.4. Scarring

Scarring in the form of tooth rakes, squid sucker hook marks, star-shaped scars and fluke holes and scallops have been reported in sperm whales previously (Berzin 1972; Stephenson 1975; Arnbom 1987). These scars appear to be common, although quantitative assessments of the frequency of these scars have not been documented. Orcas are a regular predator on marine mammals and have been documented to attack sperm whales (Arnbom *et al.* 1987; Jefferson *et al.* 1991). Sharks have also been observed around sperm whales and possible bite marks have been documented previously (Best *et al.* 1984), but again, these data are not quantitative. One possible source of the star-shaped scars found on many animals may have been wounds derived from past attacks by cookie cutter shark bites (*Isistius brasiliensis*) that have since healed. The prevalence of these scars around the head region may be due to either predation of sperm whales on this species (although this has not been documented in stomach contents previously, nor was there any evidence for this in the stomach contents analysed from these animals), or perhaps during attacks by this shark, whales may turn towards the shark in defense. The absence of these scars in younger animals and the relationship between these scars and total length suggests that whatever the cause of this form of scarring, it is something that is attained with age and takes some time to become prevalent on the bodies of animals.

2.4.5. Maxillary Teeth

Erupted maxillary teeth have been reported throughout the literature (Harrison Matthews 1938; Clarke *et al.* 1968; Berzin 1972) in varying numbers. Numbers of erupted maxillary teeth range from one to 14 and have been found in 11-50 % of animals studied, similar to that observed in this study. Harrison Matthews (1938) found no correlation between total length in whales and the number of erupted maxillary teeth, while both Clarke *et al.* (1968) and Berzin (1972) found that the number of erupted maxillary teeth increased with both age and total length. While we found no relationship between the number of erupted maxillary teeth and age, the dataset available was small and may be biased by its size.

2.5. SUMMARY

- A total of 115 sperm whales (*Physeter macrocephalus*) stranded on the west and north coasts of Tasmania largely in three mass stranding events during the month of February 1998.
- Data on the stranding behaviour, morphometrics, pigmentation patterns, presence of maxillary teeth, reproductive condition and samples of skin, blubber, muscle, stomach contents and teeth were collected from animals at the three mass stranding events. This is the first time that data have been comprehensively collected from complete or near-complete groups of sperm whales from Tasmanian waters.
- Mature females and juveniles and calves of both sexes dominated all strandings.
- Total lengths ranged from 1050.0-1150.0 cm and ages ranged from 0.75-64 years and female sperm whales from these strandings appear to be larger and older than those reported elsewhere.
- Males were older than that reported at which dispersal from female groups occurs, posing two questions: (1) do juvenile males disperse at older ages in sperm whale groups from this region? (2) do juvenile males form associations with female groups after dispersal from their parental groups?
- Females appear to have a similar reproductive cycle to sperm whales elsewhere characterized by asynchronous conception and an overlap in a gestation period of greater than twelve months with conception occurring from October to March and calving from December to April.

SECTION TWO

THE DEMOGRAPHY OF SPERM WHALE GROUPS IN SOUTHERN AUSTRALIAN WATERS.

CHAPTER THREE

THE PREPARATION OF SPERM WHALE, *Physeter macrocephalus*, TEETH FOR AGE DETERMINATION[1].

3.1. INTRODUCTION

Determination of the age of animals is essential in understanding the ecology and physiology of populations. Knowledge of the age of a population of animals provides information on demographics, growth rates, population structure and age at sexual and physical maturity (Langvatn 1995). Structures used to determine age (*e.g.* teeth) can also yield information on general health, reproductive history and the influence of environmental factors on growth, health and reproduction (Lockyer 1995a).

The teeth of sperm whales, *Physeter macrocephalus*, have been used to determine the age of individuals since the 1950s. Laws (1952) identified layers within the dentine of sperm whale teeth similar to those found in pinniped teeth and suggested they could be used for age determination. Nishiwaki *et al.* (1958) identified these dentinal layers as growth layer groups (GLGs) and suggested that two GLGs represented one year of growth for sperm whales. Limited mark-recapture studies investigating the accumulation rate of growth layers and studies calibrating seasonal changes in the thickness of the most recently formed dentine layer have been conducted (Ohsumi *et al.* 1963; International Whaling Commission 1967, 1971; Best 1970; Gambell 1977). These studies however, suggest that the rate of deposition is more likely to be one GLG per year for this species.

[1] Published as: Evans, K. and K. Robertson. (2001). A note of the preparation of sperm whale teeth (*Physeter macrocephalus*) for age determination. Journal of Cetacean Research and Management 3(1): 101-107.

Direct calibration of these assumptions is difficult. Calibration of GLGs has been established for only a small number of odontocete species. For some small cetaceans, calibration has been carried out using captive 'known-age' animals (Goren *et al.* 1987; Hohn *et al.* 1989; Hohn 1990). Tetracycline marking experiments have also enabled researchers to calibrate growth layers in some of the smaller odontocete species (Best 1976; Brodie *et al.* 1990; Gurevich and Stewart 1980; Myrick *et al.* 1988; Myrick and Cornel, 1990).

The reading of growth layer groups is not a simple procedure. Counting GLGs can be confounded by poor definition in both the dentine and cementum (Klevezal' 1980), confusion of annual growth layer groups by 'accessory bands' representing growth rates other than annual rates (Pierce and Kajimura 1980; Mikhalev 1982), and disturbances such as the mineralisation anomalies described by Lockyer (1993a; 1995a). With the aim of increasing the accuracy of counts from odontocete teeth, Myrick *et al.* (1983) defined four requirements in the preparation and reading of odontocete teeth: (1) a familiarity with the deposition and distribution of dental tissues; (2) a method of preparation that yields clear resolution of GLGs; (3) a definition of these GLGs in order to obtain consistency of counts; and (4) the representation of the amount of time associated with each GLG.

While there are several methods of tooth preparation for age determination available for use on sperm whale teeth, the most common is to section either a mandibular or maxillary tooth (usually the first or the nearest straightest and unworn) longitudinally, followed by a period of acid etching (Bow and Purdy 1966; IWC 1969; Gambell 1977; Lockyer 1980; Perrin and Myrick 1980). Teeth are rinsed with water to remove any remaining acid and air-dried before reading.

Very little has been published concerning the preparation of the teeth from young sperm whales. The smallest animal addressed in Perrin and Myrick (1980) was an 890 cm female. This lack of young individuals is due largely to the majority of material previously studied originating from whaling catches. As large animals are targeted by the whaling industry and management is based on minimum total lengths of individuals, greater proportions of samples collected from catches are those from adult animals. Small animals as a result are, for the majority, the foetuses of pregnant females.

Three strandings on the north and west coasts of Tasmania, Australia in 1998 provided us with teeth from sperm whales ranging in size from 417 cm to 1,140 cm. This chapter describes a modification to the most commonly used preparation method for the teeth of adult sperm whales. We feel that our method aids in the resolution of GLGs and therefore, in a more accurate reading of these teeth in the determination of age. We also describe a method for the preparation of teeth from young sperm whales.

3.2. MATERIALS AND METHODS

Descriptions of growth layer groups (GLGs) particular to sperm whale teeth can be found in Nishiwaki *et al.* (1958); Ohsumi *et al.* (1963); International Whaling Commission (1969); Gambell (1977); Perrin and Myrick (1980) and Donovan (1985). Definitions of terms involved in age determination were published in the Proceedings from the International Conference on Determining Age of Odontocete Cetaceans (and Sirenians) and a following workshop associated with this conference (Perrin and Myrick 1980). We used the definition published in the report from this workshop in identifying individual GLGs: 'a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine which is defined as a countable unit involving a change....from a ridge to groove' in the case of etched teeth and 'intensely stained to lightly stained' in the case of thin-sectioned, stained teeth.

3.2.1. Adults/Sub-adults

Near complete or smaller, partial lower jaws with teeth were collected from 94 sperm whales derived from three mass strandings on the north and west coasts of Tasmania in February 1998 (Chapter Two). The first mandibular or the nearest straightest tooth from 52 of these animals were prepared using sectioning and acid etching (see below). In addition, ten teeth (four from the subset of 52 and six additional teeth from the original set of 94; two of these teeth were from the same individual) were prepared for a comparative study. Of these, one half of each tooth was prepared using the methods detailed below, the other half was etched for 30 hours using the methods detailed in Lockyer (1980), to compare the effects of longer-term exposure to formic acid.

3.2.1.1. Sectioning teeth

Two methods were used for preparing teeth for sectioning:
(a) the front mandibular or nearest straightest tooth was set in polyester resin to which a hardener, methyl ethyl ketone peroxide (MEKP), was added. The tooth was placed in an appropriate vessel and oriented so that its concave curvature was uppermost before pouring the resin into the vessel. The resin was left to set overnight.
(b) the front mandibular or nearest straightest tooth was set onto a wooden block with Thermoplastic Quartz Cement Lakeside No. 70C (Hugh Courtright and Co., Illinois, USA). Again the orientation of the tooth was such that its concave curvature was uppermost.

The tooth was sectioned in half using a circular band saw set at low-speed, the cut orientated along the bucco-lingual plane, resulting in two longitudinal sections. Cutting followed the curvature of the tooth and the resulting sections followed the midline of the tooth as closely as possible. While it is common and less time consuming to use a slow rotating diamond saw to section large teeth such as those from sperm whales, the authors did not have access to such equipment. As a result, the use of a band saw was unavoidable. The authors noted that more extensive polishing is required in association with this, and so endeavored to section each tooth slightly further off centre than what is probably necessary using a diamond saw, thus compensating for the extra polishing required in achieving a polished, on-centre section.

3.2.1.2. Preparation of sections for acid etching

The most suitable half (that half closest to the mid-line of the tooth and exposing the most complete surface of the mid-line) or both halves of the tooth were polished with 150 grade sandpaper followed by 320 grade sandpaper until the majority of saw marks were removed from the cut surface.

3.2.1.3. Acid etching

The polished half section was placed in a bath of 15 % formic acid, cut surface down, and agitated to remove any air bubbles that might disrupt etching and result in uneven etching. The bath contained a minimum of 600 mL and a maximum of 800 mL of formic acid, allowing for the covering 0.5-1.0 cm of the side of the tooth. Up to seven tooth sections (depending on the size of the sections) were placed in the bath at any one time. The tooth section was kept in the bath at room temperature for a period of three hours. The section was removed and placed under running tap water for three minutes, removed

and placed in a bath of acetone for three minutes to remove any traces of acid. The tooth section was then placed again under running water for three minutes, removed and left to dry. Checks on the state of etching were made under a magnifier and the tooth section placed back into 15 % formic acid for periods of 30 minutes until a clear and complete etched surface was produced. Each bath of formic acid was only used for periods of 24 hours: the acid was discarded after this period and replaced with a fresh mixture.

3.2.1.4. Reading

Before counting GLGs, the surface of the half-section was rubbed with a soft lead pencil (No. 1 grade) to emphasize the relief of the etched surface. GLGs were counted under a magnifier. Differences in the number of GLGs estimated between halves of teeth subjected to different concentrations of acid were tested at the 95 % significance level by a t-test.

3.2.2. Juveniles/Calves

Teeth from six juvenile animals (four females, two males ranging from 417 cm to 780 cm) were prepared for aging using similar methods to those used for small delphinids (Myrick *et al.* 1983; Lockyer 1993a).

3.2.2.1. Sectioning teeth

The straightest tooth from each jaw was mounted on a wooden block with Thermoplastic Quartz Cement Lakeside No. 70C and sectioned in half using an Isomet (Buehler Ltd., Illinois, USA) low speed rotary diamond saw machine. The cut was made longitudinally to one side of the mid-line of each tooth so that two unequal halves resulted, the thicker still containing the most central mid-line of the tooth.

3.2.2.2. Decalcification

The thicker halves were placed in histological baskets and decalcified in RDO decalcifying agent (Apex Engineering Products Assoc., Illinois, USA) for three hours, agitating the specimens every one to two hours. Checks were made on the state of decalcification and the section removed or placed back into RDO and checked every subsequent hour until decalcification was complete. Decalcification was regarded as complete when the section was flexible and slightly translucent. The teeth were then flushed in running water overnight to remove any traces of the decalcification reagent. Decalcification ranged from 4 hours (428 cm female) to 30 hours (667 cm male).

3.2.2.3. Thin sectioning

Decalcified half-sections were mounted with O.C.T compound (Diagnostics Division, Miles Inc. Indiana, USA) onto a CO_2 freezing stage of a sledge microtome. The cut surface of the tooth was orientated upwards and as horizontal as possible to ensure that the straightest possible sections were achieved. Serial 35 μm longitudinal sections were cut until the mid-line of the tooth was passed and the central cavity began to reduce. A painters brush was used to remove the sections from the microtome, placing each into a petri dish of distilled water for later sorting. The thin-sections were sorted, retaining only those sections closest to the central line of the tooth and most complete.

3.2.2.4. Staining

The retained sections were placed in histological baskets, rinsed again, blotted dry and stained with Haemotoxylin for 20 minutes. Specimens were agitated in the stain to ensure complete coverage by the stain and checked for the extent of staining under a dissecting microscope. Sections were 'blued' in a 2 % ammonia solution for 30 seconds and rinsed under running water for a minimum of 30 minutes.

3.2.2.5. Mounting and reading

Stained sections were sorted again, and the most central, well-stained sections retained. Sections were floated onto a slide previously coated with a 5 % agarose/gelatin solution (this was carried out in a petri dish of distilled water to minimise the wrinkling of sections). The slides were dried on a slide warmer and permanently mounted under glass slide covers with DPX mountant (APS finechem, New South Wales, Australia). Slides were returned to the slide warmer for three to five minutes to disperse any air bubbles and then left to air dry for 24 hours. The sections were examined using a transmitted light microscope under 2-4x power

3.3. RESULTS

3.3.1. Adults/Sub-adults

The methods for acid etching detailed above yield clear, well defined growth layers in adult female sperm whale teeth (Figure 3.1).

Etching times in this study varied from a minimum of 3.0 hours to a maximum of 8.0 hours (Figure 3.2). The time taken to produce an etched surface with clear, easily discernable GLGs was found to be significantly related to the length and width of the tooth (Multiple regression, r^2=0.2, $F_{2, 45}$=3.9, P=0.03).

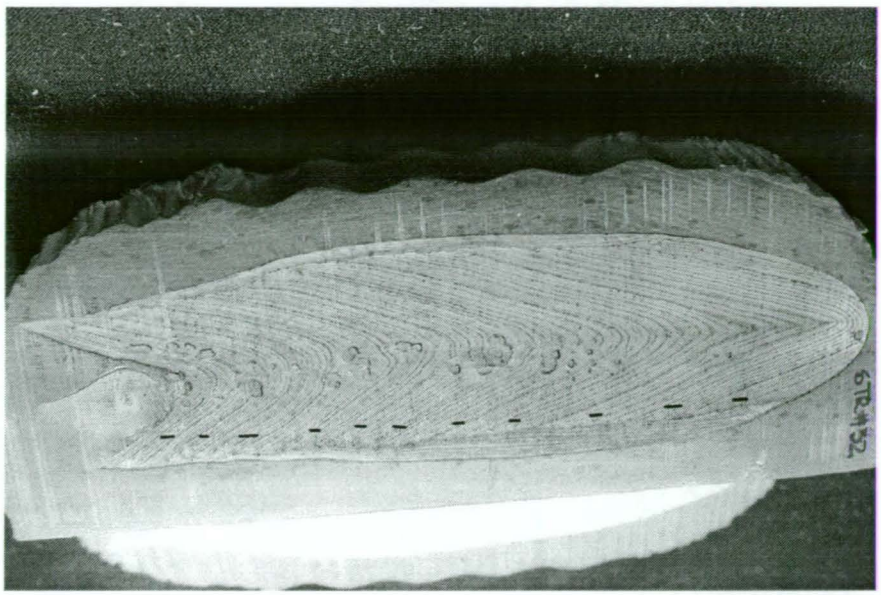
Counts of GLGs in teeth for which the two methods produced a similar etching result were not significantly different (Table 3.1). Counts of GLGs in teeth for which the exposure to 15 % formic acid produced more clearly discernable GLGs differed significantly from those in the half exposed to 10 % formic acid. Counts of the remaining teeth in which exposure to 10 % formic acid resulted in more clearly discernable GLGs were significantly different in one two cases from those in halves exposed to 15 % formic acid.

Table 3.1: Results of t-tests on sections of southern Australian sperm whale teeth exposed to the two acid-etching techniques.

Whale	10% formic acid, 30 hours			15% formic acid (exposure in minutes)			d.f.	*P*
	No. GLGs[1, 3]	Mean[2]	SE	No. GLGs[3]	Mean	SE		
STR1(3)	32	32.7	0.5	**42 (180)**	40.6	0.6	11	<0.001
STR1(34)	29	28.9	0.4	**22 (180)**	22.1	1.1	11	<0.001
STR1(37)	35	34.1	0.6	**35 (480)**	36.4	0.5	11	0.01
STR1(54)	35	32.8	0.9	**36 (345)**	35.9	0.3	11	0.004
STR2(1)	33	29.3	0.9	**33 (300)**	35.8	0.8	11	<0.001
STR2(4)	**18**	19.8	0.6	21 (405)	21.0	0.3	11	0.04
STR2(8)	**33**	39.6	2.2	39 (300)	37.8	0.8	11	0.4
STR2(16)	19	19.2	0.4	18 (420)	19.7	0.5	11	0.4
STR2(16)	20	21.9	0.9	18 (300)	22.3	0.9	11	0.7
STR2(21)	17	19.2	1.0	17 (390)	19.3	0.7	11	0.9

[1]Number of GLGs given are those values with the highest repeatability after four sessions in which the numbers of GLGs in each section were counted three times.
[2]The mean given is based on the counts from each four sessions (n=3) pooled.
[3]The method that produced sections in which GLGs were more pronounced and more clearly defined is given in bold, where there is no discernible difference no bold type is given.

A.



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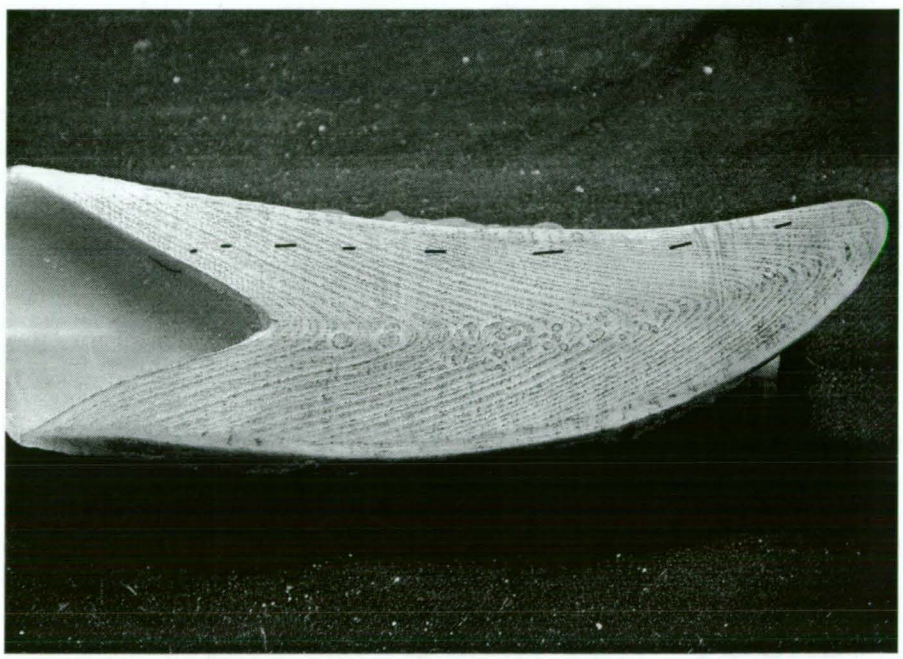

Figure 3.1: Sections of southern Australian sperm whale teeth etched with 15% formic acid showing clear, well-pronounced GLGs. The last GLG in successive groups of three is marked on each figure. (a) specimen STR1(32), 985 cm adult female, number of GLGs estimated as 35; (b) specimen STR1(36), 1,110 cm adult female, number of GLGs estimated as 26.

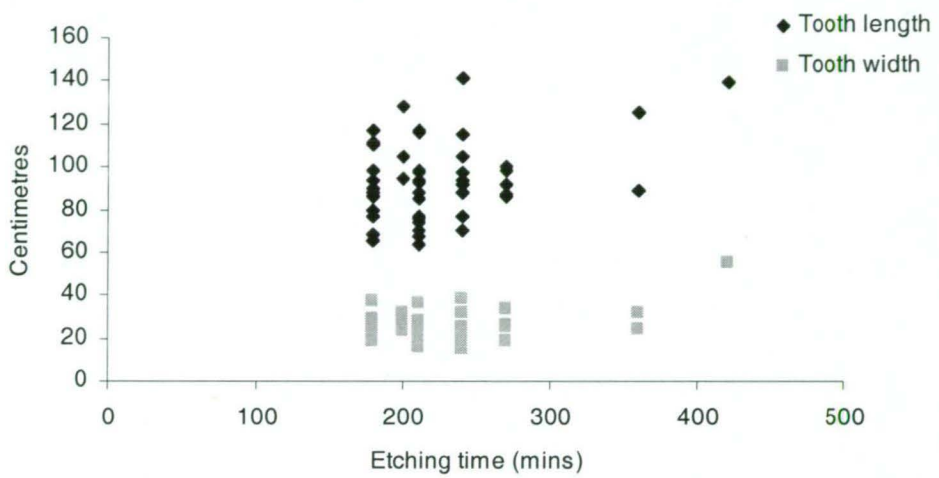

Figure 3.2: Length and width (cm) of southern Australian sperm whale teeth in relation to etching times (min).

Of the ten teeth exposed to 10 % formic acid for 30 hours, two had etched surfaces in which GLGs were more pronounced and easier to discern than those on sections exposed to 15 % formic acid, three had similar etching results (where GLGs were as equally defined) and five had etched surfaces in which GLGs were less pronounced and less easier to discern or had totally lost GLGs which were clearly visible on the sections exposed to 15 % formic acid for a shorter period (Figures 3.3 and 3.4).

3.3.2. Juveniles/Calves

The preparation of small sperm whale teeth using thin sectioning and staining yielded clearly discernable growth layer groups within the dentine (Figures 3.5 and 3.6), and provided suitable specimens for age determination.

Although not tested, acid-etching is considered to be an unsuitable method of preparation for age determination on such small teeth, possibly being too harsh. Given that four of the six animals had teeth that contained less than two GLGs (number of GLGs estimated ranged from 0.75-7.0 GLGs), acid etching is likely to be too coarse a method to discern GLGs with precision in such small teeth.

3.4. DISCUSSION

The results presented here suggest that the previously published methods involving the lengthy procedure of placing half sections of sperm whale teeth in a bath of 10 % formic acid for 30 hours at room temperature were not required to produce etched surfaces suitable for age determination.

Although the sample size restricts anything conclusive from being said about these results, as would be expected different etching results produce differing age estimates. It is possible that the extended exposure of tooth sections to formic acid may result in the over-demineralisation of the cut surface of the tooth. This would result in the production of an etched surface in which GLGs are less pronounced, difficult to discern or are totally missing, therefore underestimating the number of GLGs, or rendering the section more difficult to read or not readable at all. Such occurrences can only serve to result in inaccurate age estimations.

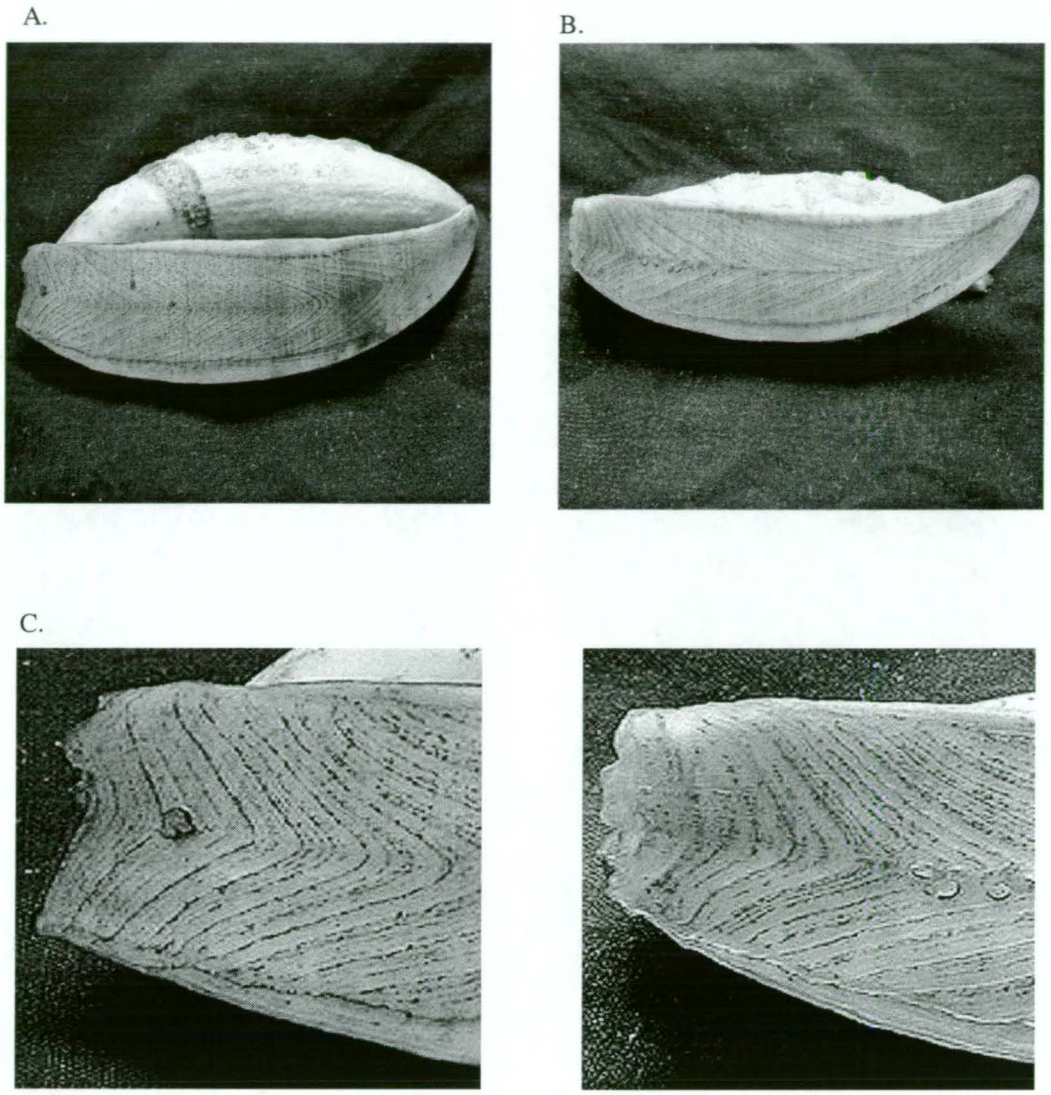

Figure 3.3: Tooth sections from STR1(3), 1,026 cm adult female sperm whale, number of GLGs estimated as 40. (a) half-section of tooth after 8 hours in 15 % formic acid; (b) half-section of tooth after 30 hours in 10 % formic acid; (c) detail of the basal portion of each tooth section: left: section etched in 15 % formic acid; right: section etched in 10 % formic acid.

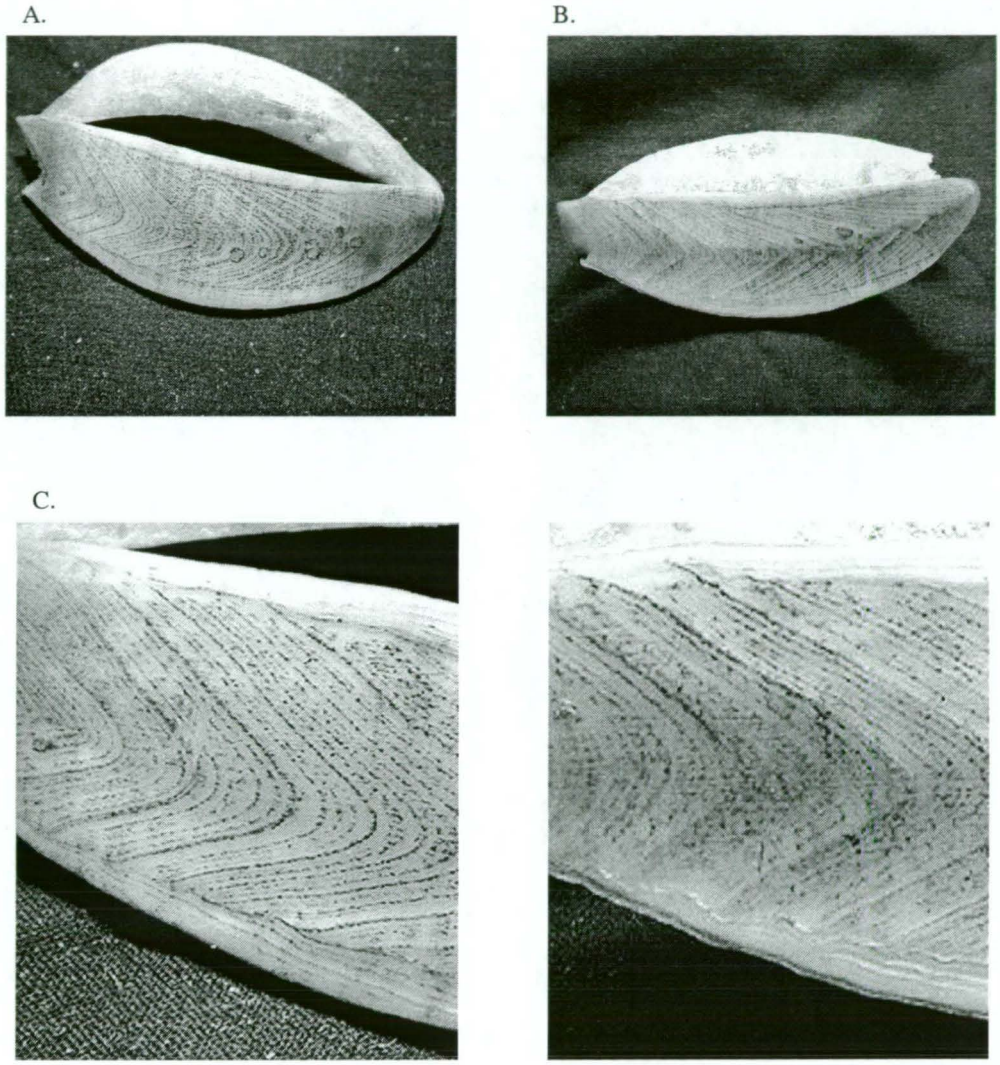

Figure 3.4: Tooth sections from STR1(54), 1,119 cm adult female sperm whale, number of GLGs estimated as 36. (a) half-section of tooth after 8 hours in 15 % formic acid; (b) half-section of tooth after 30 hours in 10 % formic acid; (c) detail of the basal portion of each tooth section: left: section etched in 15 % formic acid; right: section etched in 10 % formic acid.

The amount of time a tooth should be subjected to formic acid appears to be dependent on the tooth itself. Factors such as the size and especially the density of the tooth play an important role in dictating the amount of time taken to produce a suitably etched surface. However, it must be noted that the age of the acid used is also an important factor in dictating the time needed to produce an adequately etched surface. Re-use of acid should be kept to a minimum. The effect of the re-use of acid in etching was not undertaken as part of this study, but biases associated with this were attempted to be kept to a minimum by replacing the acid after 24 hours: a time period less than the 30 hours exposure associated with the 10 % formic acid.

We propose that half-sections of the teeth of adult sperm whales should be acid-etched for a baseline period of 3.0 hours in 15 % formic acid, checked and if required, etched further for periods of 30 minutes, checking the state of the tooth surface after each 30 minute bath. These times are similar to those proposed by Pierce and Kajimura (1980).

Teeth from small sperm whales (those animals less than 800 cm) were found to be shaped like small, hollow cones, similar to those described by Berzin (1972). Pierce and Kajimura (1980) found that in small teeth of phocoenids and delphinids the cementum tended to decalcify rather than etch when exposed to acid. While these are different taxonomic groupings of cetaceans, it may be possible that acid has a similar effect on small sperm whale teeth. As such, we consider acid etching to be too harsh on immature sperm whale teeth.

While we do not consider the methods described in this paper the only available that are suitable for use on the teeth of this species, we do consider them to yield consistently clear, well defined specimens suitable for age determination. To avoid the potential decalcification of the cementum in small teeth from young animals, such teeth should be thin sectioned and stained. Older, larger teeth can be acid etched for time periods dictated by their size and density following the guidelines above.

As demonstrated in Myrick and Perrin (1980); Stewart *et al.* (1996) and Hohn and Fernandez (1999), differing techniques used in the preparation of teeth from the same individual often result in differing age counts. Standardisation of techniques is recommended in the determination of accurate and consistent counts in marine mammals. This is essential when using the results of age determinations in life history and population biology studies, both of which are vitally important in the management of stocks of cetacean species.

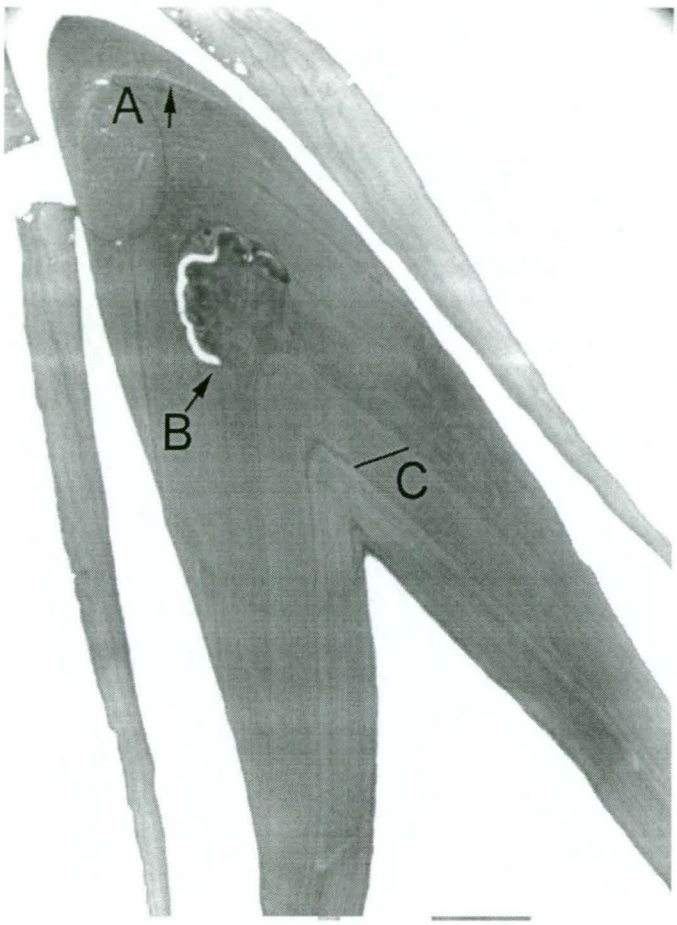

Figure 3.5: Decalcified stained section of tooth from STR2(2), 780 cm immature male sperm whale, number of GLGs estimated as 5. (a) neonatal line; (b) pulp stone; (c) growth layer group.

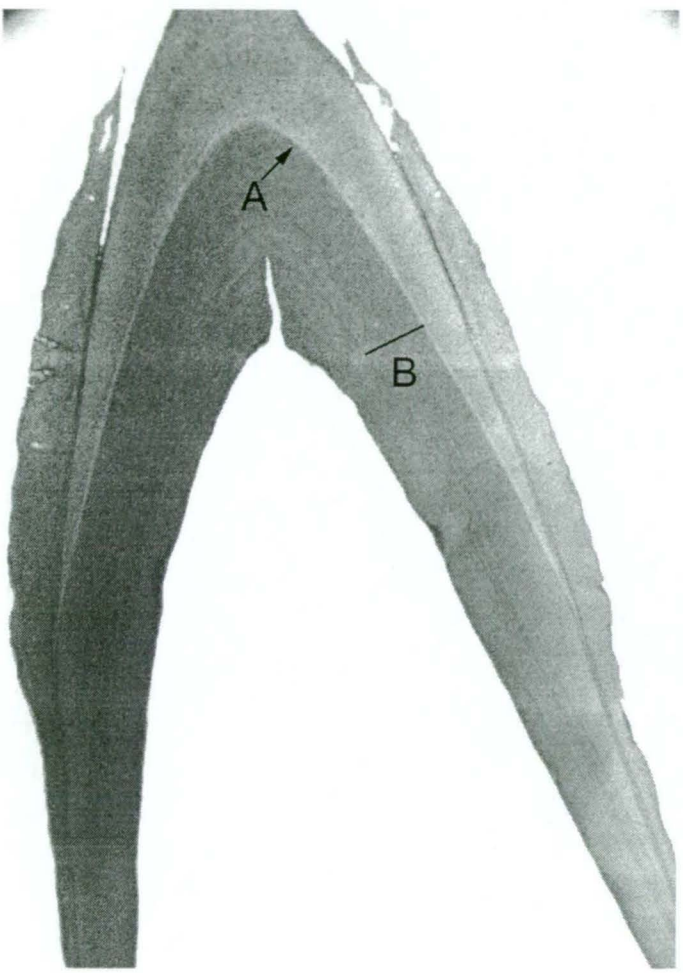

Figure 3.6: Decalcified stained section of tooth from STR2(18), 575 cm immature female sperm whale, number of GLGs estimated as 1.5. (a) neonatal line; (b) growth layer group.

3.5. SUMMARY

- A modification to the most common method of preparing sperm whale teeth for age determination involving variable etching times with 15 % formic acid is presented.
- The length of time each tooth is exposed to acid during etching is dependent on the size, and especially, the density of the tooth.
- This method yields clear, well-defined growth layers in sperm whale teeth suitable for age determination.
- A method of thin sectioning and staining of teeth is presented for use on small teeth from young animals to avoid decalcification of the cementum, which may occur if etching methods are used.

CHAPTER FOUR

FACTORS AFFECTING THE PRECISION OF AGE DETERMINATION IN SPERM WHALES, *Physeter macrocephalus*.[1]

4.1. INTRODUCTION

The determination of the age of animals is important in establishing the life history traits of individuals and populations. Integral to this is the development of an accurate age determination technique and the minimisation of any associated biases.

Growth layer groups (GLGs) in the teeth of sperm whales (*Physeter macrocephalus*) have been used to determine the age of individuals since the 1950s (Nishiwaki *et al.* 1958; Ohsumi *et al.* 1963; Gambell 1977; Rice *et al.* 1986). However, validation of the assumption that these GLGs are annual depositions, as is the case in most other marine mammals, has proven difficult. Validation techniques, such as the use of 'known-age' individuals (Hohn *et al.* 1989; Hohn 1990) and tetracycline marking experiments (Myrick *et al.* 1984; Myrick *et al.* 1988; Brodie *et al.* 1990) used in other species, have not been feasible in sperm whales because of their size and the inability to keep captive individuals. Only limited mark-recapture studies investigating the accumulation rate of growth layers and studies calibrating seasonal changes in the thickness of the most recently formed dentine layer have been conducted on this species. These studies suggest that GLGs are deposited annually (Ohsumi *et al.* 1963; International Whaling Commission 1967; Best 1970; International Whaling Commission 1971) and as a result, studies involving the age determination of this species assume that each GLG represents one year's growth (Ohsumi 1971; 1977; Lockyer 1980; Rice *et al.* 1986).

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[1] Published as: Evans, K., Hindell, M. A., Robertson, K., Lockyer, C. and D. Rice. In Press. Factors affecting the precision of age determination in sperm whales, *Physeter macrocephalus*. Journal of Cetacean Research and Management.

Another important concern associated with the aging of individual animals is that of the precision of counts of GLGs and therefore, age estimates (that is, the closeness of repeated GLG counts for the same individual). If final age estimates are the result of averaging the GLG counts from a number of reading sessions, the precision of GLG counts may have a major effect on the accuracy (the nearness of the final age estimate or GLG count to the actual age or number of GLGs) of the final estimate. As age increases, the pulp cavity in the tooth of a sperm whale fills in as a result of the deposition of further layers of dentine and eventually closes. Once the cavity is closed, the most recently deposited layers become compacted and as a consequence, become harder to discern. Mineralisation anomalies and dentinal resorption (Myrick 1988; Lockyer 1993a) may also confuse the distinctiveness of GLGs, particularly in the recently deposited dentine of older animals, which may already be compromised by the closure of the pulp cavity. A number of publications have addressed variation in the accuracy of age determination from cetacean teeth associated with the preparation and reading techniques used (Anas 1970; Hui 1980; Hohn *et al.* 1989; Hohn 1990; Hohn and Fernandez 1999). However, very few have addressed the problem of variation in precision (Mikhalev 1982; Reilly *et al.* 1983).

Variation in the number of GLGs in different teeth from the same individual may also be another source of bias in age determinations. Nishiwaki *et al.* (1958) found that teeth from both the mandibular and maxillary jaw from the same individual in sperm whales contained similar numbers of growth layers. Conversely, the Workshop on Age Determination of Odontocete Cetaceans and Sirenians found that the number of GLGs varied between different teeth from one individual (Perrin and Myrick 1980). However, the dataset was not large enough to test this statistically and it was recommended that the number of GLGs in complete series of teeth from both the mandibular and maxillary jaw of a number of individuals of varying ages be assessed. Bottlenose dolphins (*Tursiops truncatus*) were found to contain different numbers of GLGs in different teeth from the same individual (Hui 1980), possibly because teeth in the anterior of the jaw ceased depositing dentine after ten to 12 GLGs and posterior teeth ceased deposition of dentine at any time after 15 GLGs. However, both Myrick (1988) and Lockyer (1993a) found that different teeth from the same individuals in spinner (*Stenella longirostris*), pantropical spotted (*Stenella attenuata*), common (*Delphinus delphis*) and bottlenose dolphins and long-finned pilot whales (*Globicephala melas*) showed similar growth patterns yielding similar age estimates (counts in *G. melas* differed by 0-4 GLGs).

Three mass strandings of sperm whales on the west and north-west coasts of Tasmania, Australia in 1998 provided us with material with which we could investigate these problems. This chapter presents the results of investigations into variations in age estimates (i) within and (ii) between readers; (iii) between different reading methods; (iv) between different teeth derived from the same individual and (v) in relation to tooth morphology.

4.2. MATERIALS AND METHODS

4.2.1. Preparation of teeth

Near-complete or small, partial lower jaws with teeth were collected from 92 sperm whales involved in three mass strandings on the north and west coasts of Tasmania in 1998 (STR1: Ocean Beach, Strahan, n=56; STR2: Greens Pt. Beach, Marrawah, n=29; STR3: Black River Beach, Stanley, n=7; Chapter Two). The least worn and straightest first or anterior-most mandibular tooth from each individual was sectioned along the bucco-lingual plane, and one half-section polished and then etched in 15 % formic acid until clear, easily discernible dentinal layers or growth layer groups (GLGs) were produced. Teeth from calves were thin-sectioned, stained and mounted on microscope slides. Details of these methods are presented in Chapter Three.

4.2.2. Age determination

The total number of GLGs in each of the 92 tooth sections was determined three times per session across three (n=3), four (n=7) or five (n=82) sessions by a single reader (KE). The number of reading sessions was determined by the variability of GLG counts. For those teeth for which counts were not repeatable or at least two of the three counts were not close (within ±2 GLGs), counts were repeated an additional one or two times in an effort to increase the precision of of the average GLG count. Time intervals between the sessions varied from seven to 92 days. Each reading was made without reference to previous readings or additional information on individuals (*e.g.* size, sex) and teeth were read in random order during each session.

Growth layer groups were interpreted as those identified in the report of the Workshop on Age Determination of Odontocete Cetaceans and Sirenians (Perrin and Myrick 1980) as 'a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine which is defined as a countable unit involving a change from a ridge to groove' in the case of etched teeth and 'intensely stained to lightly stained' in the case of thin-sectioned, stained teeth. For those specimens in which the neonatal line could be identified (many of the teeth had worn tips and therefore were missing the enamel, neonatal line and the first few GLGs), this was not included in the total number of GLGs.

The final age estimate for each individual was determined as either the most repeated GLG count (all session estimates pooled) or, where there was no repeatability of counts (n=28) and a second reader was available (n=50; see Chapter Three) an agreed "best-estimate" after an independent reading was made by the second reader and the results from both readers were discussed. Where no second independent reading was available, the mean of all counts was used. It was assumed that skill in reading GLGs and estimating age increased with reader experience. To determine whether this had an effect on counts, a two-way ANOVA (with session number and tooth section as independent variables) was used to determine whether GLG counts differed significantly between sessions.

4.2.3. Assessment of intra-reader variation

For each tooth the standard deviation was calculated from all counts (the three counts from each of the three, four or five sessions all pooled). Following Chang (1982) and Reilly *et al.* (1983), the coefficient of variation (the standard deviation as a fraction of the mean expressed as a percentage: $CV=SDx100/\xi$) and an index of precision (the percent error contributed by each observation to the average age class: $D=CV/\sqrt{}$) were calculated. The CV and D were plotted against GLG counts to determine if there was any effect of the number of GLGs (and therefore age) influenced the precision of counts.

4.2.4. Assessment of inter-reader variation

A sub-sample containing five of the original 92 tooth sections and an associated photograph of each section were supplied to four additional readers for comparative GLG determination. All readers had previous experience in counting GLGs from sperm whale teeth. No information on the animal or the stranding from which it was derived was supplied to the readers. Readers were supplied with a standard data form and were requested to estimate the number of GLGs directly from each tooth at least three times with a minimum of five to seven days between reading sessions and without reference to

previous readings. Each reader was also requested to mark on the associated photograph of each tooth what they had interpreted and counted as GLGs, in an effort to establish areas in which variation, if it existed, occurred.

The CVand D were calculated foreach reader across each tooth to quantify individual reader precision. Actual counts from individual teeth were compared between readers using a two-way ANOVA (with reader and tooth section as independent variables). Where this test revealed that there were significant differences in GLG counts between readers, the relevant photographs (on which each reader had mapped their interpretation of GLGs) were studied and any differences in the definition of GLGs between readers noted.

4.2.5. Assessment of counts from different teeth within the same individual

For seven whales, an additional 13 teeth were prepared for age estimation (providing a total of seven teeth from each side of the jaw and a total of 14 for each animal). These animals were selected randomly from a subset of the original that contained animals from which more than seven teeth on each side of the jaw had been collected. The teeth selected were dependent on the number of teeth collected from the jaw. Where more than seven teeth from either jaw were collected, teeth were selected evenly along the length of the jaw. In all cases teeth from matching positions on both sides of the jaw were used. The number of GLGs in each tooth section was estimated using the methods detailed above without reference to other teeth from each individual. GLG counts derived from teeth on the left and right sides of the jaw in an individual were compared with a paired t-test.

An ANOVA with a Tukey HSD pairwise comparison was used to determine whether the numbers of GLGs in the 14 teeth of an individual were significantly different. For each tooth section the standard deviation, CV and D were calculated from all counts. To determine whether the number of GLGs did in fact vary between teeth in each animal, it was necessary to separate intra-reader variation in estimates from any real differences in the number of GLGs present in each tooth. D values for each tooth from an animal were plotted with the mean D calculated from the assessment of within-reader variation (the mean overall D). Where D values for each tooth were lower than the mean overall D, any variation in GLG counts were regarded as true variation in the number of GLGs. Where D values for each tooth were the same or higher than the mean overall D, variation in GLG counts were regarded as a factor of reader variation. A one-way t-test was used to test for the presence of such differences.

4.2.6. Assessment of direct tooth counts vs. photo counts

All teeth prepared (for both estimates of age of individuals in each stranding and for comparative counts of different teeth from the same individual) were digitally photographed (n=171). The number of GLGs in each tooth section was determined from an examination of these images. A paired t-test was used to compare GLG counts derived from photos against final GLG counts derived from direct readings. To determine if there was any difference in the precision of counts derived from photos and those derived from counts taken directly from teeth, a subsample of 50 randomly selected tooth images were read a further two times (for a total of three readings). Both CV and D were calculated for each method and then compared.

4.2.7. Tooth morphology

The number of pulp stones, the presence of mineralisation interferences (occlusions), and the state of the pulp cavity (whether it was open or closed) were determined for each tooth section. Anomalies were classified according to Lockyer (1993a). The CV and D calculated during age determination were log-regressed against the state of the tooth cavity and against the presence of pulp stones and regressed against the number of pulp stones to determine whether these tooth morphology factors had any effect on CV and D.

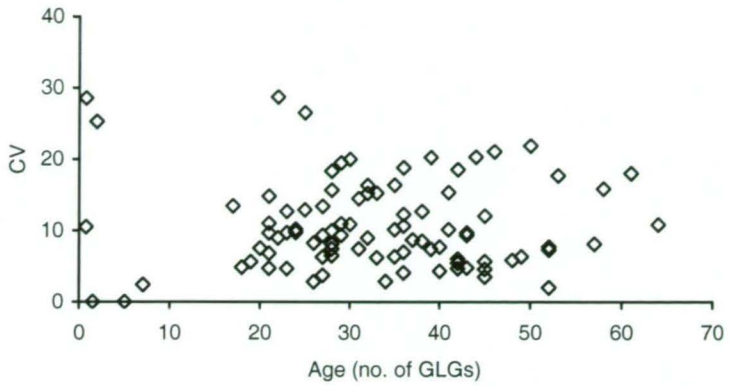
4.3. RESULTS

4.3.1. Assessment of intra-reader variation

GLG counts from sperm whales in this study ranged from 0.75 to 64.0 GLGs (mean: 32.8±13.2, n=92). There were no significant differences among GLG counts estimated in the five sessions ($F_{4, 91}$=0.9, P=0.5). For those estimates where there was no consensus of GLG counts between sessions, 89.3 % contained estimates that differed by one GLG and 96.4 % contained estimates that differed by two GLGs.

The mean CV was 10.6±6.3 and mean D was 4.8±2.9 for the reader KE. There was no significant relationship between CV or D and the number of GLGs (CV: r^2=0.001, $F_{1, 90}$=0.1, P=0.7; D: r^2=0.004, $F_{1, 90}$=0.4, P=0.6; Figure 4.1).

A.



B.

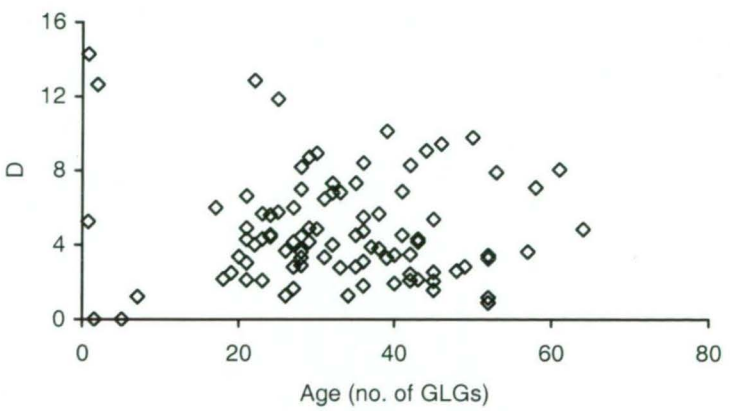


Figure 4.1: CV and D calculated from estimated number of GLGs in teeth from southern Australian sperm whales (n=92, reader=KE). (a) CV; (b) D.

4.3.2. Assessment of inter-reader variation

The difference in the number of GLGs estimated by the five readers for each of the five teeth ranged considerably between readers, from one to 21 GLGs (means: 5.0±4.9-11.8±7.7 GLGs; Table 4.1), increasing with teeth from older animals (Figure 4.2). Growth layer group counts were found to be significantly different between readers ($F_{4,16}$=2.22, P=0.02). Individual readers CV ranged from 4.8 to 12.3 and D ranged from 2.8 to 7.1 across readers.

Table 4.1: Final estimates from five readers of GLG numbers from five southern Australian sperm whale teeth, mean SD, mean CV and mean D.

	Final estimate of the number of GLGs				
Tooth	Reader 1	Reader 2	Reader 3	Reader 4	Reader 5
001	41	39	51	49	42
002	52	46	64	61	43
003	24	23	33	29	21
004	45	50	60	63	47
005	65	61	71	70	52
Mean SD	3.16	4.55	4.99	2.73	2.01
Mean CV	7.57	12.32	8.42	4.94	4.77
Mean D	2.83	7.12	4.86	2.85	2.75

4.3.3. Assessment of counts from different teeth within the same individual

No significant differences were found in the number of GLGs estimated and the CV or D calculated from readings of each tooth when the left and right sides of the jaw of individuals were compared. However, when GLG counts of individual teeth were compared significant differences were found between GLG counts in six of the seven animals (Tables 4.2, 4.3). When D values calculated from readings of each of the 14 teeth in each individual were compared with the mean D calculated from all readings (KE), significant differences were found in only two individuals (STR2(21): t_{13}=2.8, P=0.02; STR2(27): t_{13}=-3.7, P=0.003). Growth layer group counts varied increasingly with age (Figure 4.3).

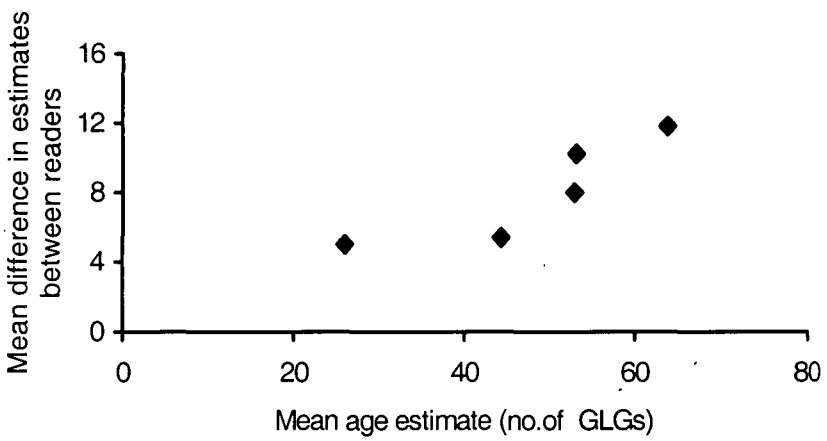


Figure 4.2: Average difference in the estimates of the number of GLGs between five readers and the average age estimated for five southern Australian sperm whale teeth.

4.3.4. Assessment of direct tooth counts vs. photo counts

Growth layer group counts derived from photographs were only available for four of the five readers. Counts derived from photographs of individual teeth were significantly higher (mean: 36.1±10.7 GLGs) than those derived from direct examination (mean: 32.9±9.5) of teeth (t_{170}=9.8, P<0.001). The mean difference in GLG counts between these two methods was 3.2 GLGs.

Of the subset of photographs that were read several times, the mean CV was 8.0±3.9 and the mean D was 4.6±2.3, while the mean CV derived from direct counts of these teeth was 11.9±5.7 and the mean D was 5.4±2.6.

Table 4.2: Mean, minimum and maximum number of GLGs, mean SD, CV and D estimated from multiple teeth (n=14) from seven sperm whales at STR2.

	Whale ID						
	1	4	8	16	21	25	27
GLG (mean)	30.9	20.6	34.2	27.8	25.3	33.4	44.8
GLG (minimum)	19.0	17.0	28.0	18.0	20.0	25.0	39.0
GLG (maximum)	52.0	25.0	43.0	37.0	32.0	43.0	64.0
Mean SD	3.5	2.9	4.0	3.6	3.7	4.0	3.6
Mean CV	11.9	13.4	11.2	13.3	14.6	13.0	8.4
Mean D	5.4	6.0	5.1	6.0	6.5	6.1	3.7

4.3.5. Tooth morphology

The mean number of GLGs in teeth with pulp stones was 36.2±11.5 (range: 5-64 GLGs, n=67) and mean number of pulp stones present was 6.4±9.7 (range: 0-53, n=92). Both the presence and number of pulp stones in tooth sections were significantly related to the number of GLGs (Presence: Log model: 2*[LL(N)-LL(0)]=17.9, d.f.=1, P<0.001; Number: r^2=0.04, $F_{1, 90}$=4.4, P=0.04; Figure 4.4). In those individuals where multiple teeth were examined, neither the presence nor the numbers of pulp stones were constant throughout different teeth (Figure 4.5). Pulp stone numbers ranged 0-32 between teeth in an individual. There was no significant relationship between either CV or D and pulp stone presence or number (Figure 4.4).

Figure 4.3: Maximum difference in age estimates from the mean age estimated derived from set of 14 teeth prepared and examined in seven southern Australian sperm whales.

The incidence of a closed pulp cavity was positively related to increasing age. Average GLG counts from animals in which the tooth examined had an open pulp cavity were significantly lower (26.4±10.4) than those of animals in which the tooth examined had a closed (45.5±8.0) pulp cavity (t_{30}=-8.4, P<0.001). In six of the seven individuals where multiple teeth were examined, the state of the pulp cavity was not consistent along the jaw; instead each contained a mixture of teeth with open cavities and closed cavities (*e.g.* Figure 4.5). The number of teeth in the jaw with closed pulp cavities increased with the number of GLGs. CV and D were not significantly related to the closure of the pulp cavity in tooth sections (CV: Log model: 2*[LL(N)-LL(0)]=104.9, d.f.=90, P=0.1; D: Log model: 2*[LL(N)-LL(0)]=104.9, d.f.=90, P=0.1).

The mean number of GLGs in teeth containing occlusions was 41.0±8.6 (range: 30-61, n=11). Occlusions were not common throughout teeth from the same individual. Of two individuals where multiple teeth were examined and occlusions were present, one of 14 teeth contained an occlusion in one animal and four out of 14 teeth contained an occlusion in the other animal.

Table 4.3: Results of ANOVAs conducted on GLG counts from multiple teeth (n=14) from seven sperm whales at STR2.

	Whale ID						
	1	4	8	16	21	25	27
d.f.	13	13	13	13	13	13	13
F-ratio	19.6	1.7	3.0	9.6	2.1	10.8	7.6
P	<0.001	0.1	0.002	<0.001	0.03	<0.001	<0.001

4.4. DISCUSSION

4.4.1. Assessment of intra- and inter-reader variation

Average CV and D calculated for intra-reader variation are similar to those presented in Reilly *et al.* (1983) for pantropical spotted dolphins and suggest that GLG counts from this dataset were relatively precise. Unlike in other studies (Doubleday and Bowen 1980; Reilly *et al.* 1983; Bjørge *et al.* 1995), this degree of precision did not decrease with increasing animal age. GLG counts did not appear to vary across reading sessions either, with no significant differences between session estimates. This suggests, at least in this study, that the precision of GLG counts was relatively constant throughout the age determination exercise.

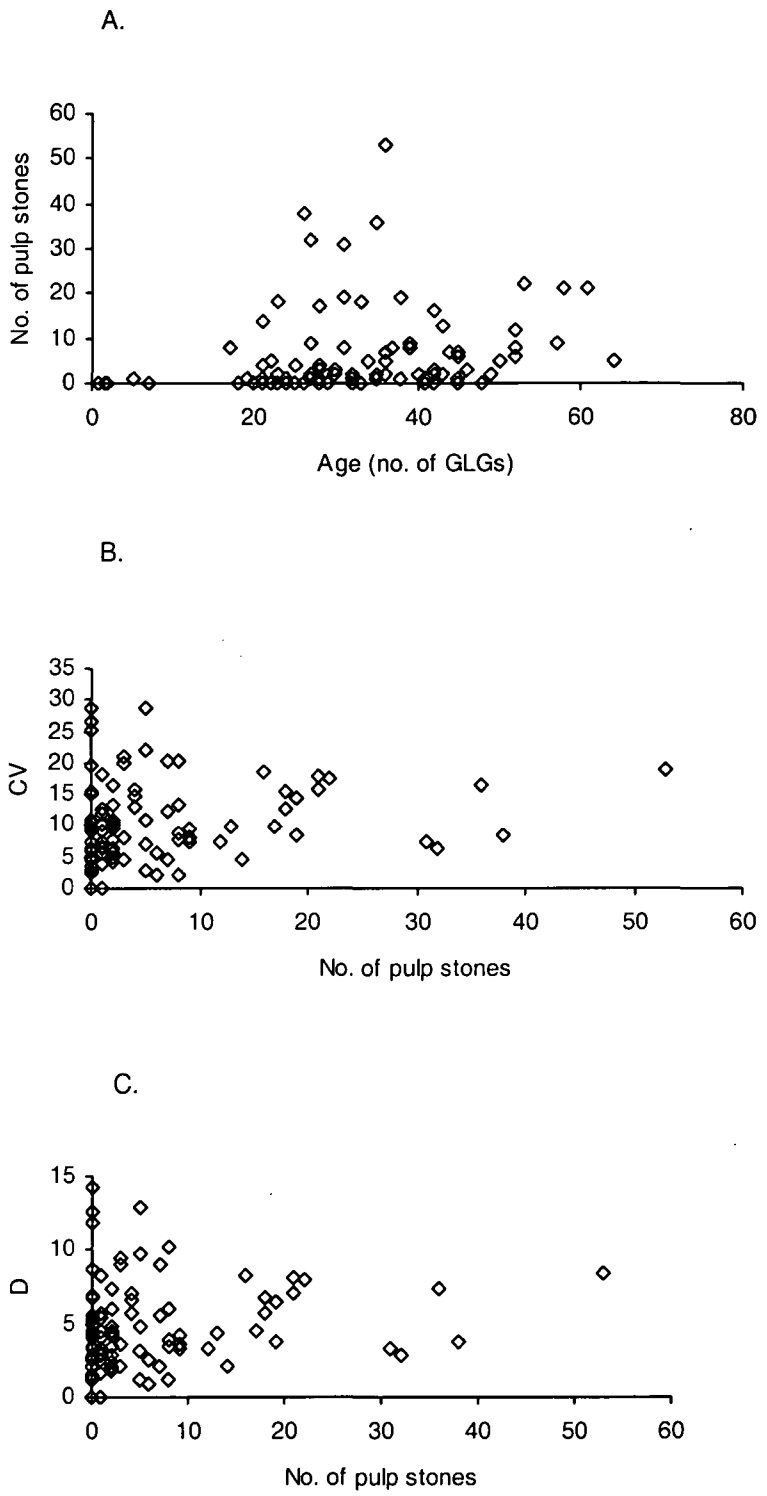


Figure 4.4: Number of pulp stones present and the estimated age, CV and D calculated from tooth sections from southern Australian sperm whales (n=92): (a) the estimated age, (b) CV and (c) D.

However, GLG counts and average CV and D varied substantially between readers (by up to 21 GLGs) and this variation increased with increasing GLG number, although again, values for CV (4.8-12.3) and D (2.8-7.1) were similar to or lower than those calculated in other studies. Mean D values in Reilly *et al.* (1983) ranged between 2.8 and 6.6, while those in Chang (1982) ranged from 3.4 to 9.8. This variation has been found to increase with increasing specimen age in a number of other cetacean species (Reilly *et al.* 1983; Bjørge *et al.* 1995; Hohn and Fernandez 1999) and is due to a decreasing ability to interpret growth structures in older animals. The deposition of growth layers becomes more highly compacted as the pulp cavity area fills in and its size decreases, making it more difficult to discern individual GLGs from one another.

None of the readings from direct examination of teeth coincided between readers, although in all at least two of the readings varied by less than three GLGs. IWC (1969) reported that the average deviations from the mean of the age estimate ranged from +4.5 to -3.1 for eleven readers examining the same teeth, although estimates for eight of the eleven readers were ±1 GLG. Donovan *et al.* (1982) reported a significant difference between the 'best' estimates of six readers when reading 50 etched teeth but no significant difference was found when four of the six readers (from the same 'school' of reading) were compared. When the age estimates of the remaining two readers were compared to the others, the average deviations from the mean were +1.42 and -1.76[1]. Mikhalev (1982) added the age estimates of two further readers experienced in reading sperm whale teeth to the results of Donovan *et al.* (1982) and observed further variation. However, he also noted that the average difference between the extreme age estimates was only 3.2 GLGs; the maximum was ten GLGs (in two teeth). These results all reveal a degree of subjectivity in the interpretation of growth layers in sperm whale teeth. The implications of this subjectivity are particularly relevant for inter-study comparisons.

Examination of the associated photographs for the cross-reading experiment also highlighted this subjectivity, showing that differences in GLG counts were due to differences in the interpretation of GLGs (*i.e.* what were regarded as accessory layers by one reader were regarded as GLGs by another; Figure 4.6). This is particularly evident when readers (b) and (c) are compared. Reader (c) appears to have interpreted all "ridge and groove" pairs as GLGs, whereas reader (b) has only interpreted the most distinct

[1] For comparisons with the present study, the mean CV for all readers was 7.55 and mean D was 1.26; for the four readers from the same 'school' the values were 4.97 and 0.83, respectively (G. Donovan pers. comm.).

"ridge and groove" pairs as GLGs. Differences are futher exacerbated by reading opposite sides of the midline in each tooth. Clarity and distinctness of GLGs can often change from one side of the midline in an etched tooth to the other. This has substantial implications when comparing age estimates between studies.

Attempts to standardise the definition and interpretation of GLGs in age determination studies were made during the International Whaling Commission's Workshop on Age Determination in Cetaceans and Sirenians. While the report of this workshop was published (Perrin and Myrick 1980) and a number of papers (Nishiwaki *et al.* 1958; Ohsumi *et al.* 1963; Best 1970; Scheffer and Myrick 1980) have provided photographs of sectioned teeth illustrating GLGs (as defined by the authors), no quantitative and objective method to assist researchers in the laboratory has yet been published. Definitions of GLGs depend, as a result, on the interpretation of the individual or the laboratory at which age estimates are being determined and are therefore, qualitative and subjective.

4.4.2. Assessment of counts from different teeth within the same individual

GLG counts from different teeth from individual whales differed significantly in six out of seven specimens. However, of these, the mean D generated from the 14 teeth in each individual was not significantly different from the mean D of the reader in five of the seven cases.

Determining whether these differences were the result of actual differences in growth structures or the result of intra-reader variation in GLG counts is confounded by the effects of differential tooth wear. Hui (1980) found that anterior teeth in bottlenose dolphins yielded lower numbers of GLGs than posterior teeth. It may have been that, rather than these teeth containing varying growth structures, differential use and therefore differential wearing of these teeth may have resulted in varying GLG counts. If differential wear does have a significant impact on the determination of GLG counts in different teeth from the same individual, determining whether growth structure variation does occur between teeth becomes difficult. One possible wasy of establishing whether there is variability in the growth structure of teeth in an individual may be to assess the microstructure of multiple teeth from an individual. The newest growth layers in a tooth occur next to the pulp cavity. Assessment of those layers closest to the pulp cavity for commonality in microstructure would establish the presence of any variability in the growth structures. Tetracycline experiments suggest that, at least in some dolphin species, different teeth in the same individual display virtually identical patterns in

growth structures (Myrick *et al.* 1984). This replication of growth structures across teeth is reported to be so exact that even if two animals of the same age are compared, their teeth can be discerned (Myrick 1991). If this replication also occurs in sperm whales, variability in age estimates can only be the result of intra-reader variability or tooth wear or a combination of the two.

Reducing intra-reader variation and thereby increasing the precision of GLG counts as well as devising some means by which tooth wear could be quantified would assist in establishing the source of this variation in GLG counts between teeth from the same individual. A larger formal internationally organized trial should be considered to quantify such factors and establish means by which these can be calibrated across studies.

4.4.3. Assessment of direct tooth counts vs. photo counts

Differences of up to 21 GLGs between readers have serious implications for the validity of comparative studies, particularly in this long-lived species, where there are no real means of verifying ages (*e.g.* via known-age animals or tetracycline experiments). However, the use of photographic techniques in the determination of GLG counts may serve to reduce this variation. Both the overall variation in estimates relative to the mean (CV) and the error contributed by each observation (D) decreased in GLG counts derived from the multiple counts of photos when compared to estimates derived from direct counts.

The higher counts produced by all readers using photographs may be the result of two factors: (i) less confusion in interpreting between GLGs and accessory layers or (ii) greater clarity of and contrast in growth structures causing accessory layers to appear as substantial a growth structure as GLGs. When counting GLGs, the reader must make a decision as to whether a growth structure is a GLG or an accessory layer. Readers may either be cautious, only interpreting the most clear structures as GLGs (and thereby perhaps underestimating the true number of GLGs), or may interpret most growth structures as GLGs (possibly including the clearest and most highly contrasted accessory layers as GLGs). This interpretation is highly subjective, but the fact that all readers counts increased while the individual reader CV values decreased when using photographs, suggests that the photographs resulted in the same effect on reader interpretation of growth structures and overall, increased reader precision.

A.

B.

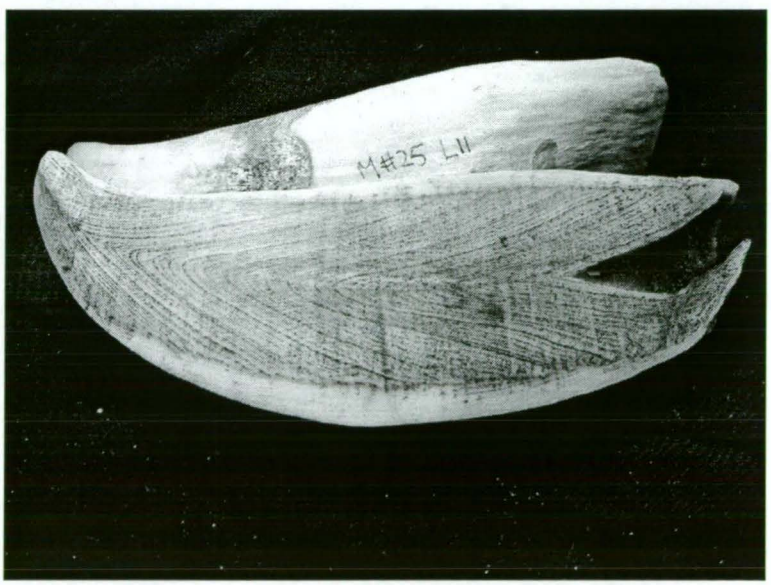


Figure 4.5: Differences in mineralization anomalies and the state of pulp cavity between two teeth from STR2(25). (a) left jaw, tooth 1; (b) left jaw, tooth 11.

Hohn (1980) found that in comparing the use of polarised light, microradiography and scanning electron microscopy in age estimation techniques, scanning electron microscopy provided images in which GLGs were easiest to read. This was attributed to the higher contrast in topographic relief between the layers of each GLG. Bow and Purdy (1966) also found that the use of photographs of etched teeth increased contrast and maximized shadow detail between growth layer groups with the end result of decreasing errors in counts. While only the effect of the use of high quality photographs on GLG counts was studied here, other photographic methods such as the use of 3-D stereographic techniques should be considered in efforts to increase the clarity of and the contrast between individual GLGs and the contrast between GLGs and accessory layers, thereby increasing reader precision.

4.4.4. Tooth morphology

Mineralisation anomalies such as pulp stones and occlusion events have been documented in cetaceans on numerous occasions (Klevezal' and Myrick 1984; Myrick 1988; Lockyer 1993a; 1995a), but no assessment has been made on the effect of such anomalies on age estimation.

Pulp stones are discrete events within the dentine of tooth sections, in most instances having little effect on the appearance of GLGs. Large pulp stones can bend GLGs, or may obscure that part of the GLG situated in the area of the pulp stone. Regardless of pulp stone size, GLGs can still be identified in the dentine of tooth sections. As a result, it would be expected that such events would have little effect on the precision (as we found here) or the accuracy of GLG counts. Occlusions however, may obscure GLGs by disrupting lamina formation to the extent that they are no longer clearly defined. This may not affect the precision of GLG counts, since the same number of laminae actually defined within and outside the mineralisation interference area can be identified. However, such events have implications for the accuracy of GLG counts, especially in older animals in which both the incidence and the number of mineralization anomalies are higher. Similarly, closure of the pulp cavity and the subsequent compacting and obscuring of GLGs is less likely to affect the precision of GLG counts (as found here), but is likely to affect the accuracy of GLG counts.

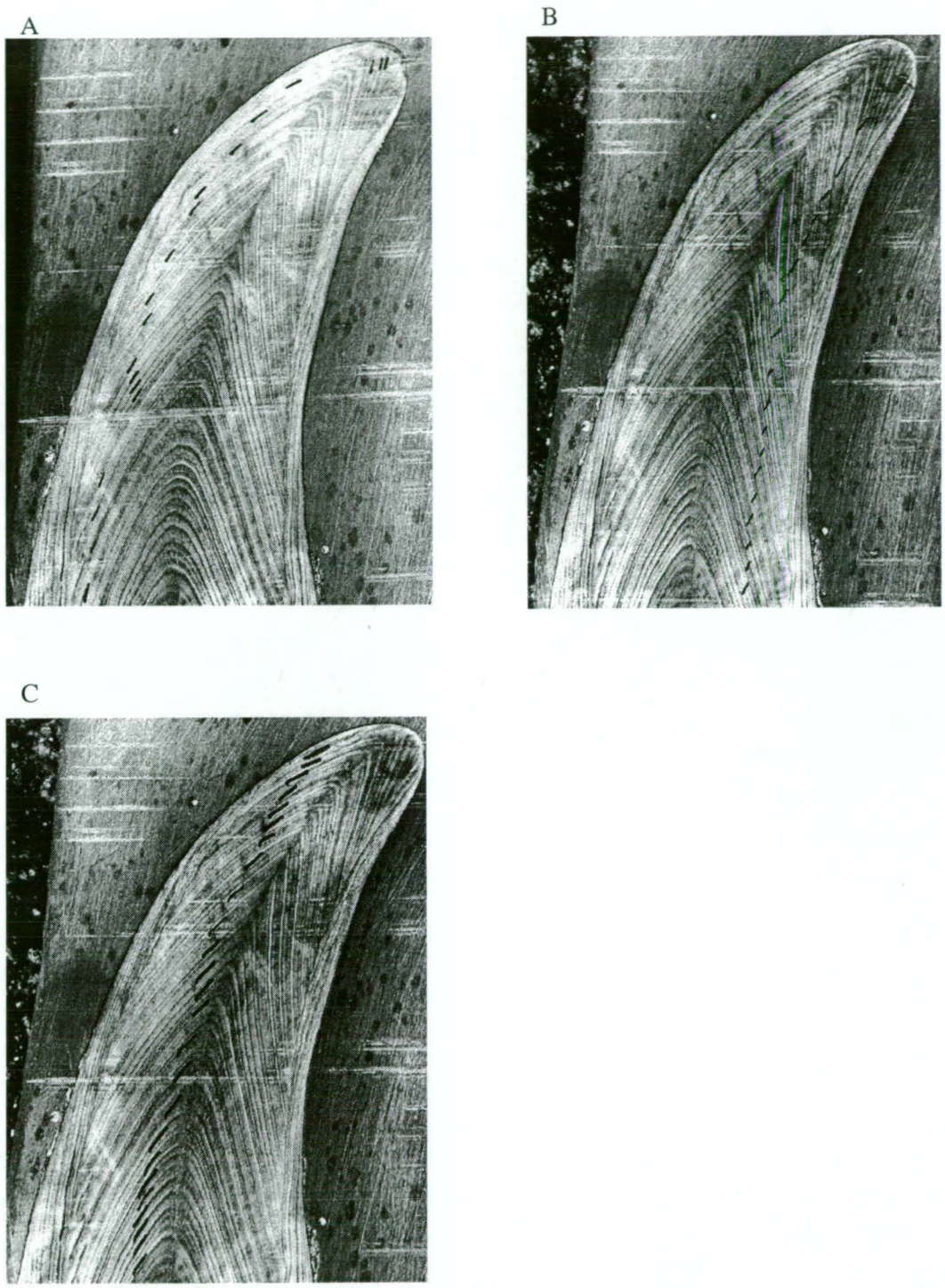


Figure 4.6: Growth layer groups in a sectioned tooth from STR2(25) as interpreted by three readers. (a) reader 1, estimated number of GLGs: 57; (b) reader 2, estimated number of GLGs: 50; (c) reader 3, estimated number of GLGs: 61.

Within the same individual, the presence and extent of mineralisation anomalies and the closure of the pulp cavity in differing teeth can be highly variable. Pulp stones form in the pulp and may not necessarily be incorporated into the dentine, or may spend varying amounts of time in the pulp before deposition in the dentine (Lockyer 1993a). As a result, varying numbers and positions of pulp stones in teeth from the same individual, as observed in this study are likely to occur (Figure 4.6). If possible, rather than collecting a particular tooth from the jaw of an animal, several teeth should be collected and age estimates determined from the tooth with the least wear, the most highly defined growth layer groups, the minimum extent of mineralisation anomalies and, if possible, with an open pulp cavity (ensuring that GLGs have not become obscured with the closure of the cavity).

GLG counts and as a result, age estimates in this species are determined by an individual reader's interpretation of growth structures in tooth sections. Therefore, the largest factor affecting the precision of age estimates of individual animals is inter-reader variation in this interpretation. GLG counts generated by a single reader can only be regarded as relative and comparable within a study, because any error introduced by the reader can be assumed to be relatively consistent across all estimates.

However, large inter-reader variation compromises the ability to compare GLG counts and therefore, age estimates between studies, especially when no indication of the precision of those age estimates is provided. While there are currently no accurate means of determining the number of annual growth layers in this species (*e.g.* via known-age animals, tetracycline experiments), attempts should be made to increase the precision of age estimates, both within and between studies, and to devise more objective means by which GLG counts and therefore, age estimates can be generated. The use of high quality photographs or other photographic techniques enabling clearer definition of GLGs are potentially a means by which greater precision in counts can be attained both within and between readers. Such photographic techniques could be used to verify GLG counts with other readers, ensuring interpretation of the same structures and facilitating 'consensus counts' generated by a number of readers, thereby increasing confidence in comparing age estimates between studies. Further studies investigating possible variability in growth structures between teeth from individuals and those enabling the separation of the effects of reader variability and the effects of differential wear in teeth on this variability should be initiated. Greater collaboration between investigators working on studies requiring age estimation of this species should be encouraged and is essential if standardization of growth structure interpretation is to be achieved.

4.5. SUMMARY

- (i) intra- and (ii) inter-reader precision in GLG counts; (iii) possible variation in growth structure deposition between different teeth within the same individual; (iv) the use of photographs to identify and count GLGs and the effect of this technique on the precision of counts and (v) mineralisation anomalies in tooth sections and the possible effects these may have on GLG count precision were investigated.
- Average CV and D calculated for intra-reader variation suggested that GLG counts from this dataset were relatively precise and that precision was relatively constant throughout the age determination exercise.
- GLG counts and average CV and D varied substantially between readers, reflecting the subjectivity of age estimates. Differences in final counts between readers appeared to be the result of differing interpretation of GLGs and this was the largest factor affecting the precision of GLG counts.
- GLG counts between teeth in the same individual varied. However, it is possible that this variation was due to intra-reader variation rather than variation in the development of growth structures, but establishment of this cause is confounded by differential tooth wear.
- Use of photographs appeared to reduce both the overall variation in estimates relative to the mean (CV) and the error contributed by each observation (D) and may have increased the definition of growth structures.
- It is therefore suggested that high-quality photographs of tooth sections be used to verify GLG counts with other readers, resulting in 'consensus counts' generated by a number of readers, ensuring interpretation of the same structures and confidence in comparing GLG counts produced in different studies.
- The incidence of mineralisation anomalies and the closure of the pulp cavity increased with increasing GLG counts in individuals, but were not consistent between teeth from the same individual and did not appear to affect the precision of GLG counts.

CHAPTER FIVE

THE AGE STRUCTURE AND GROWTH OF FEMALE SPERM WHALES, *Physeter macrocephalus*, IN SOUTHERN AUSTRALIAN WATERS[1].

5.1 INTRODUCTION

Models used to study the dynamics of populations are based fundamentally on representations of a population's age structure (Caughley 1977; Barlow and Boveng 1991; Caswell 2001). Determining the age structure of a population is therefore an essential first step when estimating the patterns of survival throughout populations. Further, the parameters that best describe significant changes to a population are those specific to age (Caughley 1977). Changes in the dynamics of populations are reflected in age-specific fecundity rates, age at sexual maturation and often the growth patterns of individuals in the population (Masaki 1980; Best *et al.* 1984; Stewart and Lavigne 1984; Caswell 2001; Fujiwara and Caswell 2001). Changes in these parameters can provide an objective means of assessing a population's resilience to environmental stresses (Caughley 1977; Hanks 1981). Such assessments are essential for effective management of populations.

Sperm whales (*Physeter macrocephalus*) are the largest of the toothed whales (Rice 1989), characterized by significant sexual dimorphism, with females attaining lengths only two-thirds that of males. Sexual differences are not confined to size alone, and exist in other aspects of sperm whale life history, most notably in their social organization and distribution. Females and immature individuals associate socially in stable units of around 13 animals based on mixed matrilines and long-term associations (Whitehead *et al.* 1991; Christal and Whitehead 2001; Mesnick *et al.* 2003). The relatedness of these units suggests that at least a proportion of females probably remain with their close relatives for long periods, if not during their entire lifetime (Whitehead and Weilgart 2000). The presence of animals not related to any others in the unit and the stability of

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associations observed in units suggests that bonds are established and maintained over substantial periods of time. These units merge and separate with others, forming temporary associations that in turn, merge and separate to form temporary larger aggregations for periods of time (Whitehead and Kahn 1992). Males conversely, disperse from their natal units, associating in groups of 12 to 15 individuals of a similar size (Best 1979). As males grow, the aggregations they are associated with become less concentrated and eventually mature individuals become largely independent of each other (Best 1979; Whitehead and Weilgart 2000).

Sperm whales have a cosmopolitan distribution (Rice 1989). Females and immature individuals range large distances throughout waters from the tropics to around 40-50°S (Rice 1989; Gaskin 1973). Males appear to have much larger ranges than females and move progressively into higher latitude waters with increasing age, reaching waters close to the ice edge (Rice 1989).

Sperm whales demonstrate slow growth rates and slow attainment of sexual maturation which in females occurs at around ten to 13 years, [although pregnancy had been reported in animals as young as seven years (Best *et al.* 1984)] and in males at around 18-21 years (Rice 1989). Physical maturity is not attained until 25-45 years in females and 35-60 years in males (Rice 1989) and life spans can reach 70-80 years (Ohsumi 1966). The average reproductive cycle of a female sperm whale is in the order of four to six years and involves a gestation period of 14 to 16 months, followed by a lactation period of approximately two years. Resting periods between reproductive cycles are thought to be between 0.75-2.75 years, and subsequently, a female might be expected to produce only four to five calves in her lifetime (Best *et al.* 1984).

Sperm whales were a large component of both shore-based and pelagic whaling operations in Australian waters from the early nineteenth century until shore-based whaling ceased in 1978 (Bannister 1974). Whaling grounds offshore of Western Australia were initially utilized by American whalers predominantly in the colder months (Townsend 1935) and these grounds were later to become the basis for shore-based whaling operations at Albany and Canarvon, Western Australia. Additionally, during the 1960s, large catches of sperm whales were also taken off Tasmania and in the Tasman Sea by pelagic factories *en route* to and from the Antarctic whaling grounds (Gaskin 1973; Bannister 1974). Limited marking studies (Brown 1981) and aerial surveys (Bannister 1969) suggest that the two whaling areas were not representative of different stocks and the two areas of exploitation are therefore considered to have impacted on the

one stock.

However, little has been published on the life history of sperm whales in this region and what has been published is only representative of exploited populations. These data additionally provide little insight into the age structure and sociality of individual pods. In order to better understand the dynamics of sperm whale populations, including changes in populations post-whaling, it is important that life history data are collected across all individuals within social groups and from currently unexploited populations (Waters and Whitehead 1990).

Longitudinal studies elsewhere have used capture-recapture and census techniques to determine demographic parameters in other cetaceans such as bottlenose dolphins (*Tursiops truncatus*; Wells and Scott 1990), orcas (*Orcinus orca*; Brault and Caswell 1993), bowhead whales (*Balaena mysticetus*; Zeh 1995) and humpback whales (*Megaptera novaeangliae*; Barlow and Clapham 1997). Census techniques lend themselves to populations that can predictably be found in particular areas such as resident pods of some of the smaller cetaceans (*e.g.* bottlenose dolphins, orcas) or larger baleen species following specific migration paths (*e.g.* humpback, bowhead whales). However, the largely pelagic existence of sperm whales and the lack of knowledge on the existence of particular ranging or migratory routes limit the ability to use such techniques in investigating the post-whaling life history of this species. Demographic parameters have been calculated from length data using photogrametric techniques for a post-whaling population of sperm whales in the Galapagos Islands area (Waters and Whitehead 1990), but little else has been published on post-whaling demographic parameters for this species, particularly on the basis of age-specific parameters.

Three mass strandings of largely female groups of sperm whales on the west and north coasts of Tasmania in February 1998 provided a unique opportunity to investigate aspects of the growth and age structure of the female component of this species in the south-eastern Australian region. In particular, these strandings provided for the collection of information from complete or near-complete social groups of sperm whales rarely obtained either because only part of any group of animals can be sampled due to their behaviour or logistical restrictions at mass stranding events.

This chapter investigates the age structure of the female component of these three strandings for which age estimates were available, (i) determining survival of mature females, from these age data and (ii) comparing these to data from an exploited population of sperm whales from waters off Japan. It also investigates growth in female sperm whales (i) calculating growth curves; (ii) comparing growth calculated from two growth models and (iii) comparing growth to that calculated from an exploited population from the western Australian region.

5.2 MATERIALS AND METHODS

Males older than five years of age were not included in this study. Males are thought to disperse from natal groups between six and ten years (Best 1979; Richard *et al.* 1996). Consequently we considered the inclusion of males in the three stranding groups older than 5 years to not be representative of the age and social structure of female groups of sperm whales. A description of the complete age structure of the three stranding groups is provided in Chapter Two. Males were not included in the calculation of growth curves due to small numbers of individuals involved in samples (n=2).

5.2.1. Age determination

Near-complete or mid-sections of lower jaws with teeth were collected from 86 individuals derived from female sperm whales groups involved in three mass strandings on the north and west coasts of Tasmania in 1998 (STR1: Ocean Beach, Strahan, n=55; STR2: Greens Pt. Beach, Marrawah, n=22; STR3: Black River Beach, Stanley, n=7). The least worn and straightest first or anterior-most mandibular tooth from each individual was sectioned along the bucco-lingual plane. One half-section of each tooth was polished and then etched in 15 % formic acid until clear and easily discernible dentinal layers or growth layer groups (GLGs) were produced. Teeth from calves were thin-sectioned, stained and mounted on microscope slides. Full details of the preparation methods are given in Chapter Three.

Growth layer groups in each tooth section were counted under a magnifier, in the case of etched teeth, and with a transmitted light microscope under 2-4x power in the case of mounted thin sections. These counts were repeated over three to five sessions without reference to previous readings or additional information on individuals (*e.g.* size, sex) and teeth were read in random order during each session. The final age estimate for each individual was determined as either the most repeated GLG count, or where there was no

repeatability of counts, the mean of all counts. Details of the determination of age estimates are given in Chapter Four.

5.2.2. Survival

Because animals less than 20 years were largely missing from this dataset, the age structure of this component of the population could not be considered to be representative of the larger population (see Discussion for further details). As a result, calculation of survival was restricted to that component of the dataset older than 20 years. These data were assumed to be representative of a static sample from a larger population, because individuals from these strandings were all sampled within the same month at the end of summer across a small geographic area. As a result, all individuals were pooled.

5.2.2.1. Demographic parameters

Static life tables were constructed for all females from age structure data. Observed age frequency data were converted to a cumulative frequency distribution representing the number of individuals observed to be alive in each age group from an initial cohort size of 78 (*i.e.* the number of whales older than 20 years in the study). Because age classes often violated the requirements of a static life table [*i.e.* that the frequency of each age class x is equal to or greater than $x + 1$ (Caughley 1977)], the age distribution was smoothed using a logistic model before constructing the life table. This provided those age classes with values and meeting the requirements of the static life table. This model is based on the equation:

$$\text{Log}f_x = a + bx + cx^2 + dx^3 + \ldots\text{etc.} \qquad \text{(Caughley 1977).}$$

Where f_x is the sampled frequency of age x and a, b, c and d are constants. The model smooths the data in a stepwise fashion, with the first step calculating $\text{Log}f_x = a + bx$ and assumes that the mortality rate is constant with age. If the ratio of the reduction in the sum of squares due to fitting this regression to the mean square of the remainder is significantly greater than unity, the hypothesis of constant mortality with age is rejected and the regression $\text{Log}f_x = a + bx + cx^2$ is then calculated. This process continues until there is no further significant reduction in the sum of squares with the addition of further terms.

The parameters of the life table calculated based on those published in Caughley (1977) were:

l_x: the survival or the probability at birth of surviving to the exact age x;
d_x: the frequency of mortality or the probability of dying during the age interval x, x+1;
q_x: the mortality rate or the proportion of animals alive at age x that die before age x+1;
p_x: the survival rate or the proportion of animals at age x that survive to age x+1.

Underestimation of the age of older animals is a potential source of error in age-based studies, particularly in a long-lived species such as the sperm whale for which there are no present means of validating ages. While age estimates in this study were found to have a high degree of precision (Chapter Four), the effects of tooth wear (which was present on all teeth from individuals older than 20 years) and occlusion events (mineralisation interferences) on the accuracy of age estimates is largely unknown. The underestimation of age estimates has implications for age-specific demographic parameters and may bias estimates of survival particularly in older age groups of animals.

In order to account for the effects of underestimation of age estimates on age-specific demographic parameters, we modelled a scenario involving random, differential tooth wear and occlusion events on the group. Based on observations of wear noted during age determination (Evans *et al.* unpublished data) we allocated an additional one to 12 years to the age of individuals. For animals >20≤40 years, we assumed low to moderate amounts of tooth wear and randomly allocated an additional one to three years to their age. For animals >40 years we assumed moderate to heavy tooth wear and randomly allocated an additional three to five years to their age estimate. Earlier studies on the effects of tooth morphology on age estimate precision (Chapter Four) identified that 13 % of all aged animals contained occlusion events in tooth dentine at an average age of 41 years. Consequently in animals >40 years we additionally randomly allocated an extra five to seven years to the age estimates of a sample of 13 % randomly identified from the group. Life tables were then calculated from the resulting age frequency. We randomised this scenario 100 times and compared the resulting mean survival to that derived from the original age estimates.

5.2.2.2. Comparison of demographic parameters with other populations

Published data on age frequencies of female sperm whales from whaling catches off the coast of Japan were collated from Ohsumi (1966). Life tables were constructed as detailed above. Survival was then compared between the differing populations of sperm whales by plotting estimated age-specific survival with 95 % confidence intervals for each group and comparing age-specific survival with a paired t-test at the 95 % significance level.

5.2.3. Growth

The total length of each whale was measured to the nearest centimetre in a straight line from the tip of the upper jaw to the deepest part of the notch in the fluke following Norris (1961). Lactation status was determined by applying pressure to teats and through the identification of the presence of milk via the *in situ* dissection of mammary glands.

Growth in cetaceans has been described using both von Bertalanffy (von Bertalanffy 1938) and Gompertz (Laird 1969) growth equations (Lockyer 1978; Cockcroft and Ross 1989; Bloch *et al.* 1993; Ferrero and Walker 1999). We present both here in an effort to establish whether either equation describes growth more appropriately in female sperm whales. The equations for these models are:

von Bertalanffy model: $L_{(t)}=L_{\alpha}\{1-\exp[-k(t-t_0)]\}$ (1)

where:

$L_{(t)}$ is the length at age (t);

L_{α} is the asymptotic length;

k is the growth rate constant;

t_0 is the age at which length is zero;

Gompertz model: $L_{(t)}= L_{\alpha}\exp\{a[1-\exp(-\alpha t)]\}$ (2)

where:

$L_{(t)}$ is the length at age (t);

L_{α} is the asymptotic length;

a is the specific rate of exponential growth (asymptotic length);

α is the rate of decay of exponential growth.

5.3. RESULTS

5.3.1. Age determination

The age of south-eastern Australian female sperm whales ranged from 0.75 to 64 years (mean=34.3±12.6, n=84; Table 5.1) with the majority of females (77 %) aged between 20 and 45 years (Figure 5.1). Associated dependent males (n=2) were estimated to be 1.9 and five years. All groups lacked individuals between the ages of eight and 16 years.

5.3.2. Survival

5.3.2.1. Patterns of survival

Survival did not change significantly under any of the 100 randomisations of age structure (ANOVA, $F_{99,5690}$=0.2, P=0.99; Figure 5.2). Modelling for the effects of tooth wear resulted in an increase in the mean survival calculated from the original age structure of mature female sperm whales of 0.905±0.046 up to 0.927±0.04. The divergence in survival produced by the model between observed and modelled age classes appears to be greatest between the ages of approximately 35 and 45 years. This divergence was reduced somewhat in older age classes. Across the 100 randomisations, average survival ranged in south-eastern Australian sperm whales from 0.905±0.048 to 0.927±0.04 with minimum survival ranging from 0.858 to 0.873 and maximum survival ranging from 0.990 to 0.992. Based on these comparisons, we felt that the median of these Monte Carlo simulations was likely to be a closer representation to the age structure of both groups of sperm whales than estimates of age in which the effects of tooth wear and occlusion events were not accounted for. Therefore, the life table parameters calculated from these age randomisations is presented as that for both the south-eastern Australian group of sperm whales and the Japanese group and used in comparisons.

Table 5.1: Total dorsal lengths (cm) and ages (year) of female sperm whale groups from three mass strandings, Tasmania, Australia (does not include males older than five years).

	Total dorsal length			Age		
Group	N	Mean±SD	Range	N	Mean±SD	Range
STR1	63	1045.8±144.2	417.0-1200.0	56	31.5±11.8	0.75-53.0
STR2	26	1033.5±114.8	575.0-1130.0	23	36.6±15.8	1.5-64.0
STR3	10	1089.1±30.4	1044.0-1140.0	7	40.3±13.8	22.0-61.0
All	99	1046.9±129.7	417.0-1200.0	86	33.6±13.3	0.75-64.0

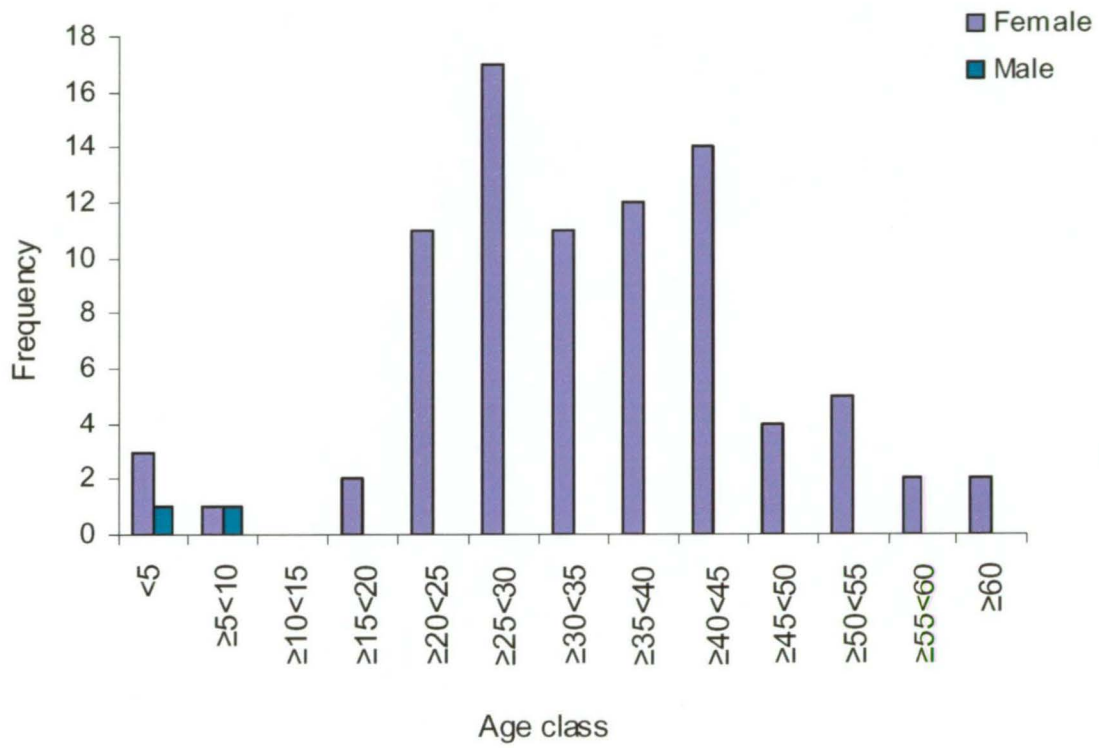

Figure 5.1: Age distribution of female sperm whale groups involved in three mass strandings, Tasmania, Australia.

The basic life history parameters for mature south-eastern Australian female sperm whales are presented in Table 5.2. Survival in this group of animals appears to be high and relatively constant throughout life (mean=0.921±0.045 range: 0.866-0.991; Figure 5.3). The greatest decrease in survival appears to occur in mature females between the ages of 25 to 50 years (a decrease from 0.976 to 0.876). The rate of decrease in survival is reduced in age classes over 50 and becomes relatively constant in age classes over 55 years.

5.3.2.2. Comparison of survival with other populations

The age of female sperm whales derived from Japanese whaling data ranged from two to 77 years (mean=22.1±11.4, n=2235; Figure 5.4).

Survival of mature female sperm whales from Japanese waters followed a similar pattern to that of south-eastern Australian whales, with relatively constant and high survival throughout life (Figure 5.3). Average survival in sperm whales from Japanese waters (mean=0.888±0.036; range=0.862-0.977) was significantly lower than that observed in female sperm whales from south-eastern Australia (t_{55}=9.5, P<0.001). Comparison of the 95 % confidence intervals around the survival curves of the two groups of sperm whales demonstrated a similar survival at the age of 20 years, but a sharper decline in the survival of whales from Japanese waters to the age of approximately 45 years, followed by similar survival to that observed in Australian sperm whales in older age groups (Figure 5.3).

5.3.3. Growth

Total dorsal lengths of female sperm whales ranged from 417.0-1,200.0 cm (Table 5.1) with animals 1,050-1,200 cm in length comprising 68 % of all animals (Figure 5.5).

Growth in female sperm whales, as described by both the von Bertalanffy and Gompertz equations in this study, is rapid up to a length of approximately 1,000 cm and about 16 years, after which the growth rate declines and reaches an asymptotic length shortly after 1,100 cm and 19 years (Figure 5.6). Both pregnancy and lactation as observed in this group of animals, appears to occur after asymptotic length is attained (Figure 5.7)

Table 5.2: Observed and predicted frequencies with age and life table for southern Australian female sperm whales.

Age (year)	Observed frequency	Predicted frequency	lx (survivorship)	dx (mortality)	qx (mortality rate)	Px (survival rate)
20	78	75.37202	1	0.009143	0.009143	0.990857
21	78	74.68293	0.990857	0.010394	0.01049	0.98951
22	77	73.89953	0.980464	0.011782	0.012016	0.987984
23	74	73.01152	0.968682	0.013311	0.013742	0.986258
24	73	72.00822	0.955371	0.014984	0.015683	0.984317
25	71	70.87888	0.940387	0.016796	0.01786	0.98214
26	69	69.61296	0.923592	0.018739	0.020289	0.979711
27	68	68.2006	0.904853	0.020797	0.022984	0.977016
28	64	66.63307	0.884056	0.022949	0.025958	0.974042
29	62	64.90339	0.861107	0.025161	0.029219	0.970781
30	55	63.00698	0.835947	0.027393	0.032769	0.967231
31	54	60.94229	0.808553	0.029597	0.036605	0.963395
32	49	58.71149	0.778956	0.031715	0.040715	0.959285
33	47	56.32103	0.747241	0.033687	0.045081	0.954919
34	45	53.78201	0.713554	0.035446	0.049675	0.950325
35	43	51.1104	0.678108	0.036931	0.054461	0.945539
36	42	48.32687	0.641178	0.038084	0.059397	0.940603
37	36	45.4564	0.603094	0.038859	0.064433	0.935567
38	35	42.52751	0.564235	0.039224	0.069516	0.930484
39	33	39.57115	0.525011	0.039161	0.074592	0.925408
40	32	36.61947	0.48585	0.038676	0.079604	0.920396
41	30	33.70441	0.447174	0.037787	0.084501	0.915499
42	29	30.85635	0.409387	0.036532	0.089236	0.910764
43	28	28.10286	0.372855	0.034962	0.093767	0.906233
44	27	25.46774	0.337894	0.033134	0.098061	0.901939
45	25	22.97035	0.30476	0.031114	0.102093	0.897907
46	21	20.62523	0.273646	0.028965	0.105847	0.894153
47	20	18.44211	0.244681	0.026747	0.109314	0.890686

Table 5.2 continued.

Age (year)	Observed frequency	Predicted frequency	lx (survivorship)	dx (mortality)	qx (mortality rate)	Px (survival rate)
48	19	16.42613	0.217934	0.024516	0.112491	0.887509
49	18	14.57834	0.193418	0.022317	0.115383	0.884617
50	15	12.89625	0.171101	0.02019	0.118	0.882
51	12	11.37449	0.150911	0.018163	0.120354	0.879646
52	12	10.00553	0.132749	0.016256	0.12246	0.87754
53	11	8.78025	0.116492	0.014484	0.124338	0.875662
54	11	7.68853	0.102008	0.012853	0.126003	0.873997
55	9	6.71975	0.089154	0.011365	0.127476	0.872524
56	7	5.86314	0.077789	0.010017	0.128774	0.871226
57	6	5.10812	0.067772	0.008805	0.129917	0.870083
58	5	4.44449	0.058967	0.00772	0.130915	0.869085
59	5	3.86264	0.051248	0.006754	0.131793	0.868207
60	4	3.35357	0.044494	0.005898	0.132554	0.867446
61	3	2.90904	0.038596	0.005142	0.133223	0.866777
62	3	2.52149	0.033454	0.004476	0.133802	0.866198
63	2	2.18411	0.028978	0.003892	0.134306	0.865694
64	2	1.89077	0.025086	0.00338	0.134744	0.865256
65	1	1.636	0.021706	0.002933	0.135128	0.864872
66	1	1.41493	0.018773	0.002543	0.135455	0.864545
67	0	1.22327	0.01623	0.002203	0.135735	0.864265
68	0	1.05723	0.014027	0.001907	0.135987	0.864013
69	0	0.91346	0.012119	0.001651	0.136207	0.863793
70	0	0.78904	0.010469	0.001428	0.136381	0.863619
71	0	0.68143	0.009041	0.001235	0.136551	0.863449
72	0	0.58838	0.007806	0.001067	0.13668	0.86332
73	0	0.50796	0.006739	0.000922	0.136802	0.863198
74	0	0.43847	0.005817	0.000796	0.136908	0.863092
75	0	0.37844	0.005021	0.000688	0.13701	0.86299
76	0	0.32659	0.004333	0.004333		

Both the von Bertalanffy and Gompertz equations provided similar fitting growth curves for female sperm whales (von Bertalanffy: r^2=0.82; Gompertz: r^2=0.83; Figure 5.6) with similar estimations of asymptotic length. The sum of residuals calculated from the Gompertz equation was lower than that calculated from the von Bertalanffy equation, (Gompterz: 240497.5; von Bertalanffy: 245288.6), however these were not significantly different (t_{83}=0.1, P=0.9).

The equations for the von Bertalanffy and Gompertz growth curves calculated from female sperm whales are:

von Bertalanffy: $L_{(t)}=1082.12\{1-\exp[-0.16(t-2.58)]\}$
Gompertz: $L_{(t)}=1080.67\exp\{1.03[1-\exp(-0.18t)]\}$

5.4. DISCUSSION

The demographic parameters described in this study are consistent with those of a mammal with a life history involving low fecundity, high longevity, slow growth rates, late attainment of sexual maturation, high input of resources into young over a protracted period and high sociality involving communal care of young and communal defence (Whitehead and Weilgart 2000). These traits define sperm whales as extreme K-selected animals (Boyce 1984). Social complexity appears to be one evolutionary strategy enabling high overall survival and is typical of a number of other long-lived extreme K-selected species such as long-finned pilot whales (*Globicephala melas*), orcas (*Orcinus orca*), African elephants (*Loxodonta africana*) and humans (*Homo sapiens*). In these species, prolonged reproductive strategies (involving lengthy lactation and offspring dependence periods and slow growth and attainment of sexual maturation) and high social complexity are closely tied and have evolved as a means of ensuring high survival rates (Whitehead and Weilgart 2000).

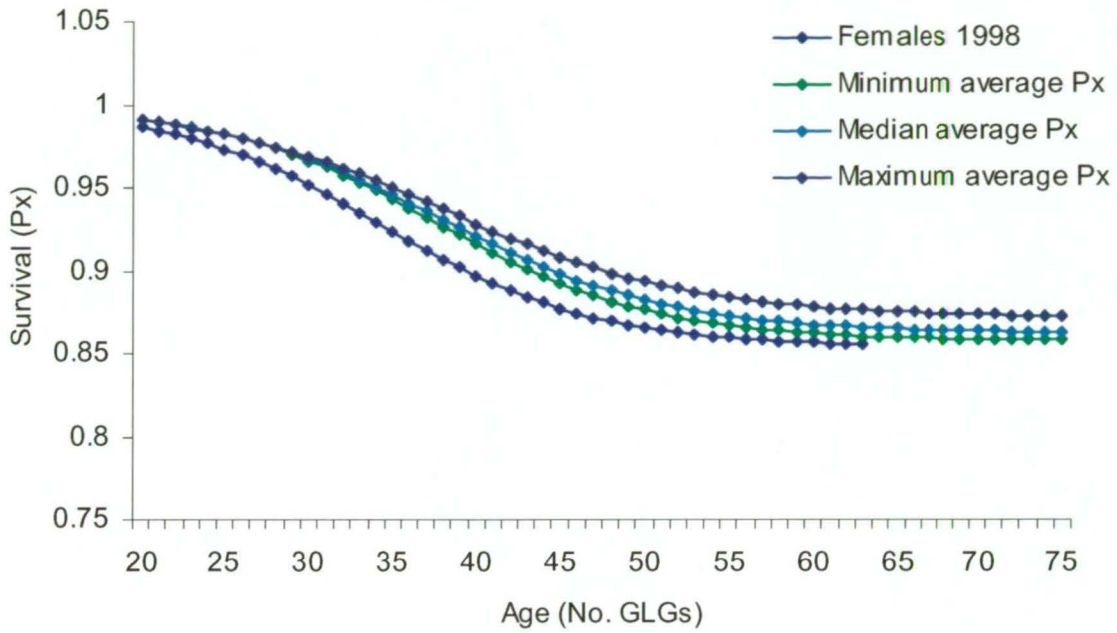

Figure 5.2: The survival of mature female sperm whales from southern Australian waters modelled under differing age structure conditions.

5.4.1. Age structure

The three groups of sperm whales that stranded in Tasmania were composed of juveniles of both sexes and adult females (Chapter Two). None of the three groups of sperm whales involved in the three Tasmanian strandings contained individuals between the ages of eight and 16 years. This may be a reflection of the small sample size presented here and consequent undersampling of age groups. However, nowhere else in the age distribution is there a lack of individuals spanning this number of years. The age structure of any population of animals at a given point in time is a factor of mortality and recruitment into that population. The lack of individuals between these ages may be the result of two factors (i) a response to changing environmental conditions or (ii) dispersal from natal groups into other female groups or into temporary associations with other immature animals, before a return to either natal groups or different groups with increasing age.

The absence of age groups in the age structure of other long-lived species such as the African elephant have been attributed to changing environmental condition (*e.g.* drought) and associated declines in food availability (Moss 2001). Declines in reproductive success have been associated with decreases in food availability in a number of pinniped species (DeLong *et al.* 1991; Trillmich *et al.* 1991; Trites 1991; Lunn *et al.* 1994) and have been postulated to also occur in cetacean species (Lockyer 1986; 1987). Failure to reproduce in only one season, given the low fecundity of female sperm whales, is likely to be reflected in the age structure of a population.

While trade-offs between maintenance and reproduction such as those that occur in elephants may occur in the life history strategy of female sperm whales, it is unlikely that such strategies would result in the age structure observed in this study. A lack of animals across a number of age groups as observed in this study, if assumed to be representative of the greater population, would indicate that the population from which these data are derived has produced almost no offspring in the last 20 years. If this was indeed the case, the population from which these animals were derived has severe reproductive failure and is in rapid decline. Rather, the lack of juveniles may be the result of dispersal of individuals from natal groups.

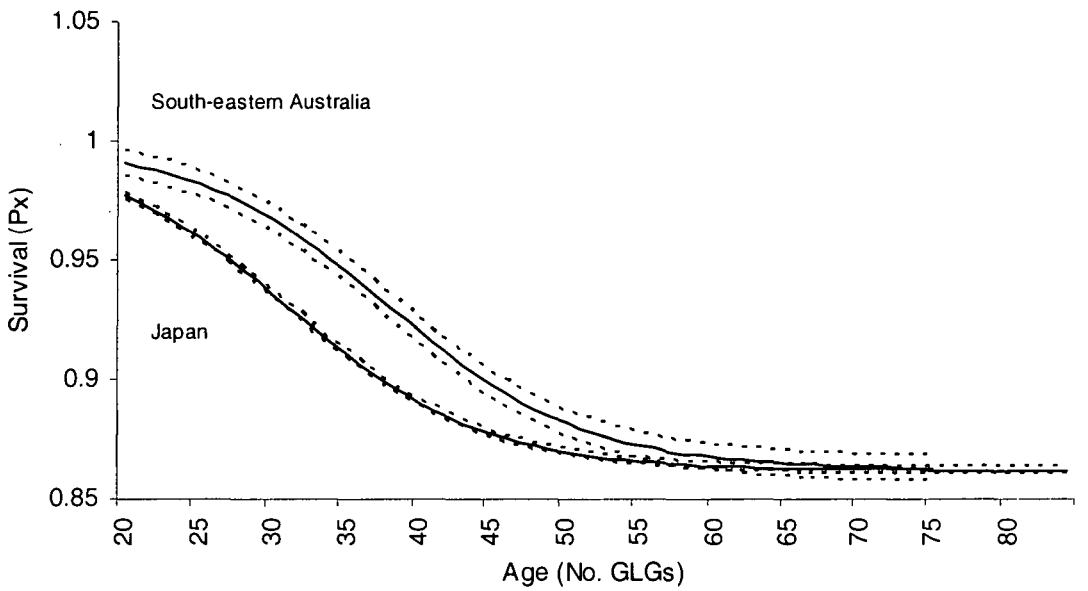

Figure 5.3: Survival curves with 95 % confidence intervals for mature female sperm whales from south-eastern Australian waters and Japanese waters (Ohsumi 1966).

Dispersal in male sperm whales and the occurrence of 'bachelor groups' of immature and maturing males have been documented extensively (Best 1979; Rice 1989; Childerhouse *et al.* 1995; Jaquet *et al.* 2000), however, the extent and timing of female dispersal is largely unknown. Genetic studies suggest there is some female dispersal, although in sperm whales, this appears to be on a much smaller scale than male dispersal (Richard *et al.* 1996; Lyrholm *et al.* 1999).

Preliminary molecular analysis of the sperm whales involved in the Tasmanian strandings suggests that these groups were comprised of both related and unrelated animals (Mesnick *et al.* 2003). First order relationships were observed between a mother and fetus pair and four adult females from STR3 and in addition second order relationships were observed between an older female and four females. However, one female within this group was observed to have no close relationships to any other individual in the group.

Genetic studies in other areas coupled with long-term photo identification studies suggest that other female sperm whale groups also contain non-related, long-term associates (Mesnick *et al.* 2003). Groups of sperm whales, including both immature males and females were reported by whalers (Best 1979), and it has been suggested that there may be dispersal of immature females into these groups, followed by a return to natal groups with increasing age (Whitehead and Weilgart 2000). Among other groups of sperm whales for which ages are available, two groups of sperm whales captured off South Africa also lacked females between the ages of six and eleven (Ohsumi 1971), and a mass stranding of sperm whales on the coast of Oregon contained no individuals less than eleven years (Rice *et al.* 1986). The lack of individuals between the age of six and eleven years also suggests some female dispersal from natal groups and therefore under-representation of these age groups in the age structure of sampled groups.

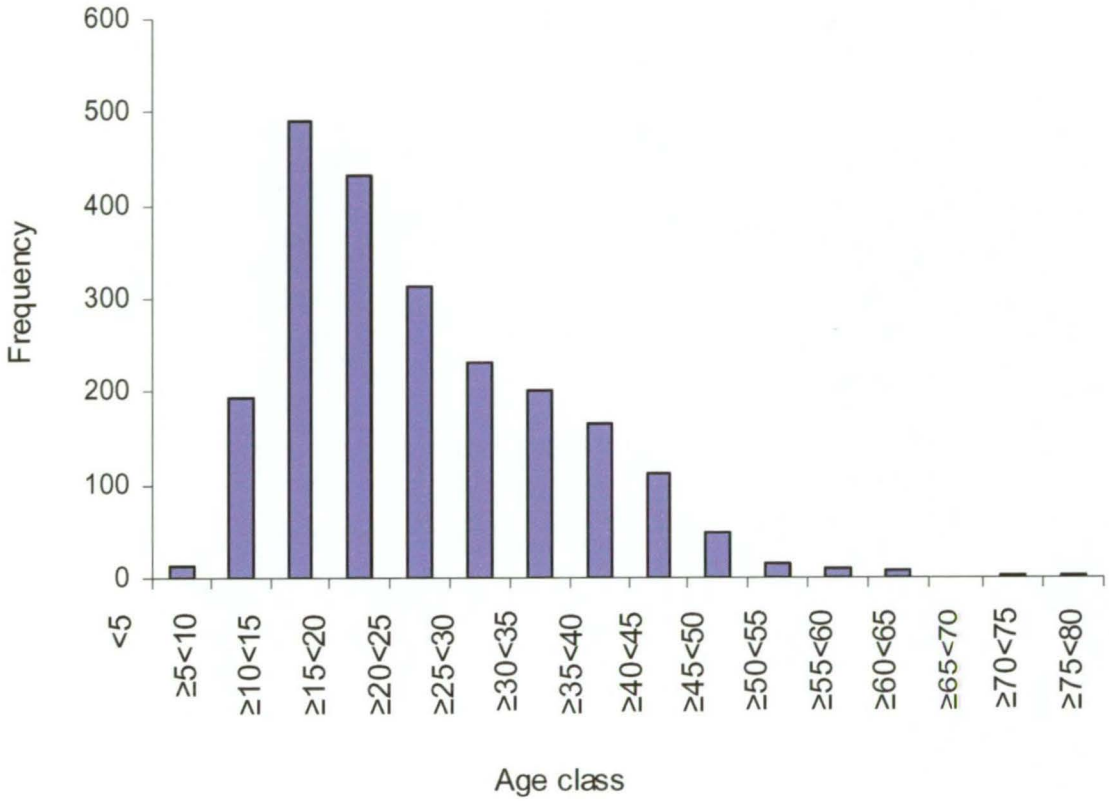

Figure 5.4: Age distribution of female sperm whales from Japanese waters derived from whaling data (Ohsumi 1966).

5.4.2. Survival

5.4.2.1. Age structure effects and biases associated with the data

Regardless of the factors influencing the age structure of female groups of sperm whales observed in this study, the age structure of sperm whales less than 20 years cannot be considered to be representative of the larger population. These data therefore invalidate any life table analyses and estimation of demographic parameters using these data cannot be made. Assuming that mortality rates between sperm whales less than 20 years and those older than 20 years is constant, it could be possible to extrapolate the age structure observed in sperm whales 20 to 40 years to that less than 20 years. However, differences in the factors controlling rates of mortality in animals less than 20 years in comparison to those older than 20 years prevent such an extrapolation. Exploitation of sperm whale populations in the Australian region ceased in 1978. Therefore mortality in all animals older than 20 years in the Australian region comprises of a combination of natural and fishing mortality, whereas mortality in whales less than 20 years is a factor of natural mortality only.

In order for the standing age distribution to be representative of the temporal age distribution, it is assumed that age specific fecundity and mortality are stable and that the exponential rate of increase has been and is currently zero (Caughley and Sinclair 1994). The age structures of real populations are often not stable, resulting in varying amounts of variation around life table parameters. In order to account for this variation, Caughley (1977) proposed a minimum sample size of 150 with which survival could be estimated accurately. However, it is often difficult to obtain such large sample sizes, particularly with large cetaceans such as sperm whales. Despite our substantially lower sample size, the survival curve demonstrated by mature female sperm whales from south-eastern Australian waters compares well to that demonstrated by the much larger sample size of female sperm whales caught in Japanese waters (n=2235). Moreover, calculation of 95 % confidence intervals demonstrated only small variability around our calculations of survival in this group of animals, suggesting the size of this sample was adequately large enough to account for variability associated with the smoothed survival curve.

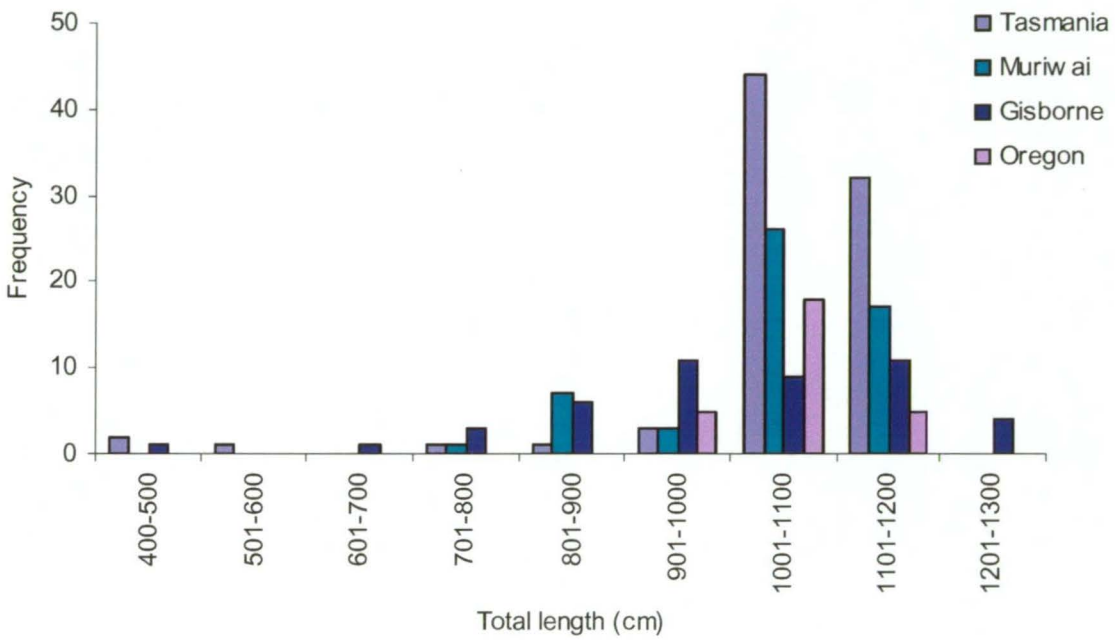

Figure 5.5: Distribution of total lengths in female sperm whale groups from mass strandings in Australia, New Zealand and North America.

Comparisons of vertical estimates of survival (based on the age structure of a population at a given point in time) against those derived from a horizontal perspective (based on the fate of a cohort followed through time) have observed overestimation in mortality rates derived from vertical analyses (Olesiuk *et al.* 1990). This is due to not only mortality influencing declines observed in older age classes, but also increases in the initial size of cohorts through time. The extent of this bias is a function of the true mortality rate and the population growth rate. Given that both datasets used in this study were derived from populations below carrying capacity and exposed to exploitation, these biases are likely to effect rates of survival calculated for both Australian and Japanese sperm whales. As a result, the survival rates presented here are tentative but do provide a basis for relative comparisons between populations.

Data derived from whaling data are subject to a number of biases, particularly those associated with selectivity of the catch, which, through the regulatory nature of the fishery, largely excluded young animals. Data derived from Japanese catch statistics are further confounded by biases associated with the reliability of these data (Kasuya 1999). These data are reported to be significantly influenced by substantial under-reporting and mis-representation of statistics derived from these catches. While calculation of survival only for the mature female portion of the population largely avoids biases associated with the exclusion of young animals from whaling data, other biases identified may influence those age structure data used in this study. However, Kasuya (2000) observed that biases reported within Japanese whaling data were largely associated with data published by the Bureau of Whaling Statistics (BIWS) and presented those published by the Whales Research Institute (WRI) as a closer representation of true catch statistics. We used age structure data derived from scientific subsamples of animals from whaling catches published by the WRI. Given the similarity in the shape of survival rates curves calculated between the Australian and Japanese datasets in this study, we have assumed that any biases associated with the age structure data from Japanese whaling data, if present, were consistent across age groups and therefore that the age structure is largely representative of the larger population.

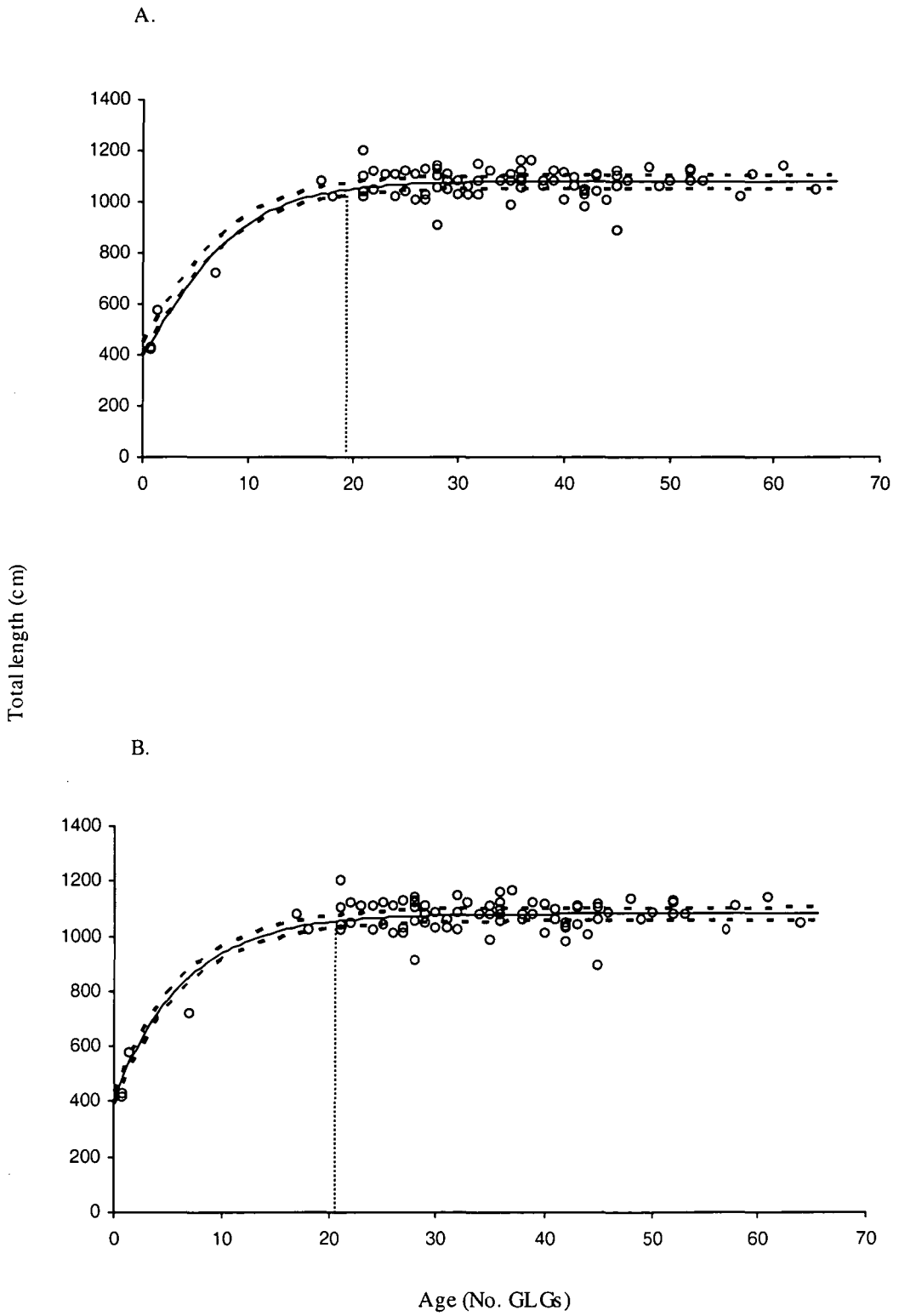

Figure 5.6: Growth curves for southern Australian female sperm whales using the (a) Gompertz; (b) von Bertalanffy equations. The dashed line defines estimated age at which asymptotic length is attained by each model.

Changes in the age structure of female sperm whales, as might be expected due to the effects of differential tooth wear and occlusion events, had little effect on the pattern of survival observed in mature female sperm whales. The overall effects of changes in age structure due to underestimation of ages as a consequence of tooth wear and occlusion events, were to reduce survival in those age groups older than 25 years and thereby increase the slope of the mortality rate. Survival rates calculated over 100 randomisations showed little deviation to survival calculated from the original age structure of female sperm whales. While the accuracy of age estimates cannot be calculated in this species due to an inability to validate age estimates (see Chapter Four), we feel that the randomisation model developed here approximates, at least to some extent, the effects of tooth wear and occlusion events on the age structure of the sperm whale groups in this study.

5.4.2.2. Patterns of survival

The greatest decrease in survival in south-eastern Australian sperm whales occurred between the ages of 20 to 45 years. Similar changes in the survival of females have also been recorded in sperm whales elsewhere, with mortality increasing from the ages of 20 to 27 years in females derived from South African whaling fisheries (Best 1970). Long-finned pilot whales and orcas also demonstrate a decrease in survival between the ages of 30 and 40 years from previous relatively stable rates of survival during the adult stage (Olesiuk *et al.* 1990; Bloch *et al.* 1993; Brault and Caswell 1993) and the greatest decrease in female elephant survival occurs at around 30 years (Woodd 1999). The stage at which this escalated decrease in survival occurs may be typical of the longevity of these species and may be associated with factors such as increases in birth-related mortality, susceptibility to predation due to commitments to the care and protection of young, greater energetic demands on females associated with pregnancy and lactation.

5.4.2.3. Comparison of survival with other populations

Average survival was substantially higher in south-eastern Australian sperm whales in comparison to whales from Japanese waters. However, although survival was statistically different between the two groups, survival in both groups was high and remained above 0.85 throughout life. Additionally, the survival curve estimated suggests that survival in individuals less than 20 years was not markedly different and approached a similarity such as that observed in individuals greater than 50 years.

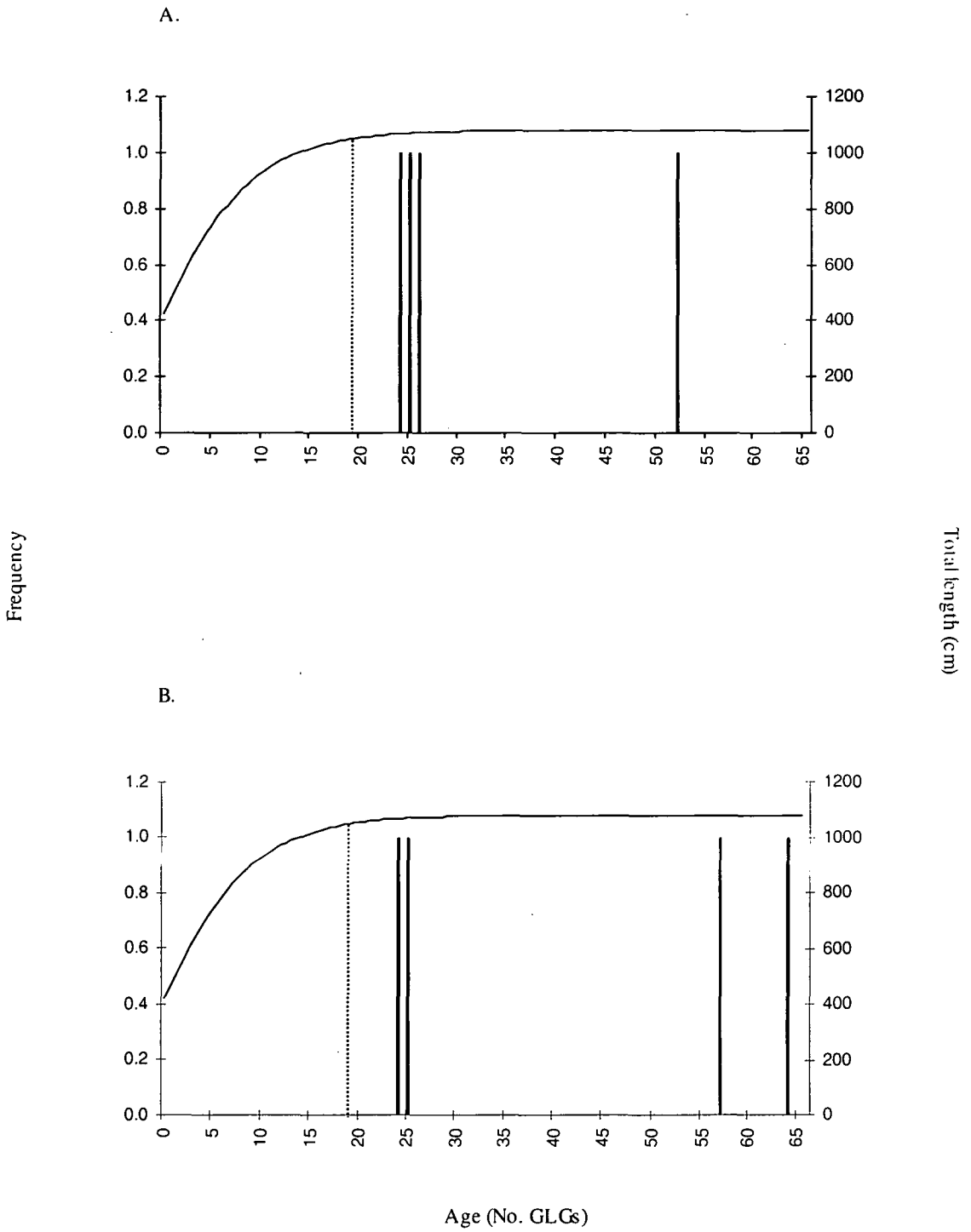

Figure 5.7: Age of (a) pregnant and (b) lactating females in relation to Gompertz growth curves for southern Australian sperm whales. The dashed line defines estimated age at which asymptotic length is attained using the Gompertz model.

Average survival in female sperm whales caught in Western Australian waters was reported as 0.92 in 1964 and 0.91 in 1965 (Bannister 1969), similar to that observed in this study, and similarly higher than that calculated in females from Japanese waters. Given that the survival rates presented in this study are derived from that portion of the population of females that was subject to some degree of exploitation, the similarity between survival rates calculated in the two Australian studies suggests that survival rates calculated in this study are indicative of the larger south-eastern Australian population of mature female sperm whales. Additionally, the younger portion of the female sperm whales derived from the stranding would have only just been born when whaling ceased in Australian waters. These animals would have spent most of their lives in an exploitation free environment. It is likely that only those animals older than 30 years would have experienced substantial exposure to exploitation. Whilst age-specific survival rates are not available for those females from Western Australian waters, the lack of difference between overall mean survival rates suggests that there has been no substantial change in the survival rate of mature females post-whaling.

The higher survival rates observed in the Australian populations in comparison with those from Japanese waters could be the result of either (i) higher rates of exploitation on mature female sperm whales in Japanese waters; (ii) differing natural mortality rates between the two populations or (iii) mis-representation of the age structure of mature female sperm whales caught in Japanese whaling catches. Deriving natural mortality figures from sperm whales is difficult due to the lack of pre-whaling life parameters and biases in catch rates and statistics (see Waters and Whitehead 1990, Dufault *et al.* 2000; Kasuya 1999; Whitehead 2002). As a consequence, it is difficult to discern the factors contributing to the differences in survival rates observed in this study.

5.4.3. Growth

Growth in cetaceans has been described using both von Bertalanffy (von Bertalanffy 1938) and Gompertz (Laird 1969) growth equations. The von Bertalanffy growth equation, traditionally an equation used to describe growth in fisheries species, has been used to describe growth in bottlenose dolphins (*Tursiops truncatus*; Cockcroft and Ross 1989), long-finned pilot (Bloch *et al.* 1993), fin (*Balaenoptera physalus*) and sei (*B. borealis*) whales (Lockyer 1978). The Gompertz equation, calculated to describe growth in mammals, has been used to describe growth in spotted (*Stenella attenuata*) and spinner (*S. longirostris*) dolphins (Perrin *et al.* 1976; Perrin *et al.* 1977), long-finned pilot whales (Bloch *et al.* 1993) and Dall's porpoises (*Phocenoides dalli*; Ferrero and Walker 1999). Both equations describe growth similarly in female sperm whales, providing well fitting

equations and can therefore be considered as equally adequate for describing growth in this species.

5.4.3.1. The Gompertz and von Bertalanffy models

The Gompterz growth model assumes that growth is fundamentally exponential with a decreasing exponential factor with length (Laird 1969). Growth as described by the von Bertalanffy equation is largely linear, with this function decreasing with length (von Bertalanffy 1938). Growth progressively decreases as asymptotic length is approached in the von Bertalanffy model, while in the Gompertz model the maximum growth rate is not necessarily at t=0 but at $t=\ln(A_0/\alpha)\alpha$, which can be greater than 0 (Bloch *et al.* 1993).

Gompertz models were observed to describe growth in long-finned pilot whales more accurately than von Bertalanffy models (Bloch *et al.* 1993), while in belugas (*Delphinapterus leucas*) the von Bertalanffy model described growth more accurately (Suydam 1999). Larger sample sizes, particularly those including substantially larger numbers of animals less than 1,000 cm may serve to determine more conclusively whether either model describes growth in this species more appropriately.

5.4.3.2. Growth in south-eastern Australian sperm whales and in other populations

Growth in female sperm whales from south-eastern Australian waters is similar to that described in female sperm whales elsewhere. Asymptotic length in the sperm whales studied here appears to be attained at approximately 20 years, several years prior to the youngest documented lactating female (24 years). Sexual maturity documented in female sperm whales from South African waters occurs between the ages of nine to13 years (Lockyer 1981; Rice 1989), and age at first ovulation from Western Australian female sperm whales has been reported to occur at 10.8 years, substantially earlier than the youngest lactating female observed here. Mean growth curves presented in Rice (1989) describe growth reaching an asymptote at around 20 years, similar to that observed in this study. However, because animals were not examined for foetuses and lactation was not determined in all females, it is impossible to determine if reproduction occurs prior to asymptotic length in this group of animals.

The majority of previously published growth curves for sperm whales have been fitted to age-length data by eye rather than through the calculation of growth curves (Nishiwaki *et al.* 1963; Best 1970; Gambell 1972; Lockyer 1981). A von Bertalanffy model was used to calculate growth curves for sperm whales from Western Australian waters (Bannister 1969), resulting in the equation:

$$L_{(t)}=1052.44\{1-\exp[-0.115(t-4.117)]\}$$

When this equation is used to determine the age at which asymptotic length is attained, an age of 56.5 years is estimated. This suggests that growth as described by this equation continues for a much longer period in those female sperm whales caught in the Western Australian fishery than it does in those in this study from south-eastern Australian waters. Asymptotic length would not be attained until well past what is reported to be both sexual [nine-13 years; Rice (1989)] and physical maturity [25-45 years; Rice (1989)], and well past the onset of reproductive activities as observed in south-eastern Australian sperm whales (Figure 5.7) and those documented elsewhere (Gambell 1972; Best 1970).

This appears incongruous to all other growth curves published for females in this species. However, when the curve derived from Western Australian females is plotted against the von Bertalanffy growth curve calculated in this study, substantial differences reflecting the source of data are obvious (Figure 5.8). Lengths up to the age of 4.5 years, as calculated by the equation published in Bannister (1969), produce negative values and are clearly unrepresentative of true growth in this species. Very few immature animals would be expected to be included in growth curves calculated from animals caught from whaling operations such as those included in Bannister (1969), due to legal length limits and restrictions on the take of females accompanied by calves. However, only growth curve parameters were reported in Bannister (1969) and no details were reported on the age structure of the animals used to calculate these parameters, so it is therefore impossible to determine whether this growth equation was calculated from data that included juvenile animals.

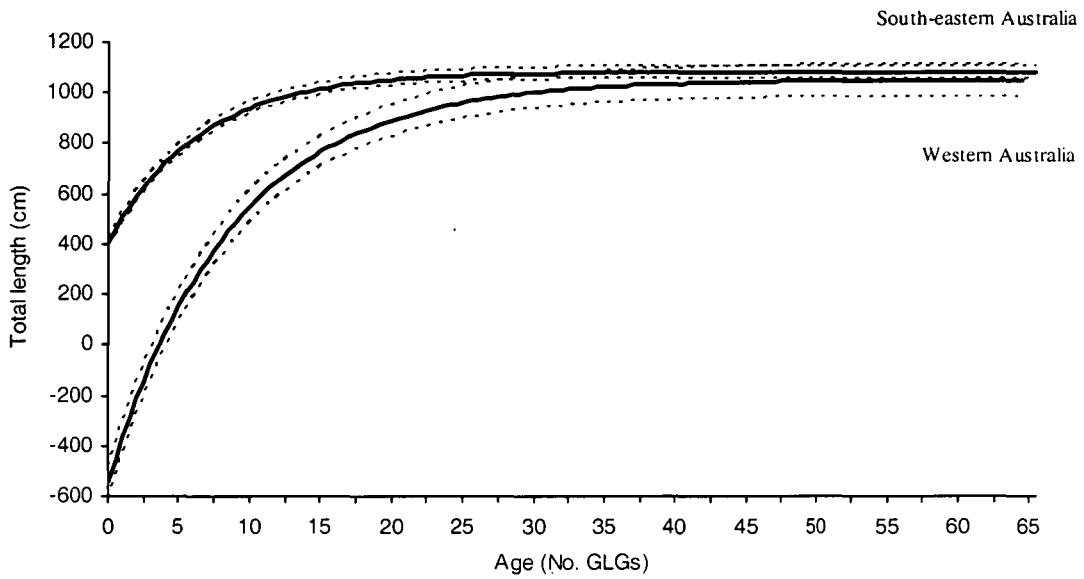

Figure 5.8: Comparison of von Bertalanffy growth equations with 95 % confidence intervals calculated in this study and in Bannister (1969).

Bannister (1969) reported that the modal length and age of male sperm whales from Western Australian whaling catches were higher than those for males elsewhere and female sperm whales from south-eastern Australian waters were observed to be on average larger and older than those documented elsewhere (Chapter Two). It has been postulated that whales from different geographic regions and genetic stocks differ in general morphology, including total length (Arnbom and Whitehead 1989, Waters and Whitehead 1990). Strandings from New Zealand contained females both of a similar average length (1057.2±107.7; Stephenson 1975) and a lower average length (1004.5±162.4 Robson and van Bree 1971) to those documented here (Figure 5.5).

Whether female sperm whales from the Australian region vary morphometrically and in their longevity to those from other areas is difficult to determine conclusively due to a number of confounding factors. Temporal differences in sampling may account for variation in the composition of groups encountered and therefore, in the average length and age of animals documented. If female sperm whale units merge and separate continuously over time, this will result in changes in the composition of groups and consequently, both geographical and temporal changes in the size and age structure of animals in these groups (Chapter Two). Differential temporal movements of different age classes of males may also have the same effect. Differential whaling effort, the biases of sizes targeted and differences in the temporal scales of whaling operations may have resulted in skews in the age and length distributions of sperm whales documented for populations in different regions.

When analysing catch data from the North Pacific, Kasuya (1991) observed increases in the total length of male sperm whales of up to 20 % during the 1970s and attributed these increases to declines in the population and subsequently, greater food resources per capita available to individuals. Observations of increased growth rates and attainment of larger sizes with increases in food availability are not novel observations and have been documented elsewhere in both cetacean and pinniped populations (Lockyer 1978, 1981; Hanks 1981; Choquenot 1991; Trites and Bigg 1992; Bell 1997).

Total lengths of females sampled from post-whaling groups of sperm whales involved in mass strandings in Oregon, USA and Tasmania, Australia were found to be significantly higher than those sampled in free ranging groups of sperm whales in the North Pacific and South Africa during the 1960s (Chapter Two). Total lengths in female sperm whales sampled from the mass stranding in Oregon in 1979 were on average 9 % and those from

south-eastern Australia were on average 11 % higher. Global sperm whale populations have been the focus of two intensive periods of exploitation, resulting in massive reductions in population numbers. Annual global catches peaked in 1964 at over 29,000 whales (Rice 1989), and in the North Pacific alone during the year 1968, over 16,000 sperm whales were caught (Ohsumi 1980). While it is difficult to assess the impacts of whaling in the Australian region due to the absence of pre-whaling population estimates, substantial numbers of sperm whales [in the order of 3-5,000 whales per year during 1960-1970; (Bannister 1974)] were removed from this area. It is possible that the larger total lengths observed here are factors of density dependent effects associated with increases in resources per capita in the Australian region.

The growth equations presented in this study are important to two reasons. Firstly, they document growth in female sperm whales from the south-eastern Australian region for the first time, and secondly they can provide a means by which temporal changes in the population of female sperm whales in the south-eastern Australian region can be assessed. If there has been, and is a continuing change in the demographic parameters of this species with the cessation of whaling and the post-whaling recovery of this species, these equations can be used for temporal assessments of the condition of the population based on the concept that a reduction in growth rates can be equated with poor condition (Hanks 1981).

While the life history of sperm whales has evolved in such a way to ensure high lifetime survival, the slow growth rates, late attainment of sexual maturity and low fecundity result in slow population growth. In a population close to carrying capacity, these life history traits are advantageous and minimise pressures on the population associated with competition for resources. However, in situations were a large proportion of the population is removed (as we have observed as a result of whaling), the ability to recover quickly is compromised and as a result, population growth is extremely slow. There are concerns that the low fecundity rate demonstrated by female sperm whales implies that post-whaling populations will not readily recover from decreases as a result of whaling and that the effects of whaling will have a longevity greater than in other more fecund species (Whitehead and Weilgart 2000). Information on younger individuals is essential for the determination of rates of survival in these age groups and the calculation of more detailed population parameters. These data are additionally essential in determining changes in survival rates and therefore rates of increase in populations post-whaling. High priority should be given to the identification of the distribution, stock identity, numbers of sperm whales and critical habitats for this species in this region in an effort to

establish the impacts of exploitation and recovery patterns of this species. Knowledge of these parameters is essential in identifying both present and potential pressures on populations in the Australian region. Furthermore, the relationships and interactions of sperm whales in the Australian region with adjacent populations should be established. The determination of the flow-on effects of whaling and subsequent patterns of recovery cannot be undertaken unless the impacts on a population throughout its entire spatial and temporal range can be assessed (Taylor 1999; Clapham and Hatch 2000).

5.5. SUMMARY

- Life tables and age-specific survival were calculated from the age structure of mature female sperm whales involved in three mass strandings on the Tasmanian coastline in 1998.
- In comparison to life table and demographic parameters calculated from a group of sperm whales caught in whaling operations off the coast of Japan, both groups were observed to demonstrate high lifetime survival.
- Australian mature female sperm whales demonstrated significantly higher survival rates than mature females from Japanese waters and similar survival to female sperm whales reported from whaling operations conducted in western Australian waters, suggesting little change in survival post whaling.
- Growth equations using Gompertz and von Bertalanffy models calculated described growth in female sperm whales similarly and growth resembled that of female sperm whales observed elsewhere.
- Changes in the demographic parameters of female sperm whales with the cessation of whaling may be reflected in the growth rates of individuals observed in this study, and as such, these equations may provide a useful tool for monitoring continuing changes in the demographic parameters of this species.

SECTION THREE

ENERGY ACQUISITION AND UTILISATION IN SPERM WHALES FROM SOUTHERN AUSTRALIAN WATERS.

CHAPTER SIX

THE DIET OF SPERM WHALES, *Physeter macrocephalus*, IN SOUTHERN AUSTRALIAN WATERS[1].

6.1. INTRODUCTION

With the management of recovering whale populations a high priority for national and international environmental managers (Taylor and Dizon 1999), and the need to derive better understanding of energy flow and trophic links in marine systems due to increasing fisheries pressure and global warming (Brodie and Påsche 1982; Simmonds and Mayer 1997), a more comprehensive understanding of the diet of marine predators, particularly large top-order predators is needed. In order to quantify natural variations in the foraging relationships of predators within an ecosystem, these assessments must be conducted over appropriate temporal scales and for wide-ranging and migratory species, assessments must also cover appropriate spatial scales. However, attaining quantitative assessments of the diet of pelagic, wide-ranging, deep diving predators such as sperm whales (*Physeter macrocephalus*) is difficult.

Cephalopods are a key trophic link in the Southern Ocean ecosystem and form an important part of the diet of many marine animals including whales, seals, birds and fish (Clarke 1983). It has been estimated that in the Southern Ocean alone, some 34 million tons of cephalopods are consumed by vertebrate predators annually and nearly 12 million of this specifically by sperm whales (Clarke 1983; Rodhouse 1989). Dietary information for sperm whales has been derived from stomach contents collected from a small number of beach-stranded and numerous whaling industry derived animals throughout the Southern Hemisphere (Gaskin and Cawthorn 1967; Clarke *et al.* 1976; Clarke 1980; Clarke and MacLeod 1982; Pascoe *et al.* 1990; Clarke and Roeleveld 1998). However, information on the diet of this species in the Southern Ocean is still sparse.

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[1] Submitted to ICES Journal of Marine Science as: Evans, K. and M. A. Hindell. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters.

While some studies have conducted limited spatial and temporal assessments of the diet of sperm whales from particular areas (Kawakami 1980; Santos *et al.* 1999; Smith and Whitehead 2000), data derived from whaling operations are often biased towards adult animals, particularly males, and disregard any dietary assessments on smaller spatial scales, especially in terms of individual pods or groups.

Diet studies other than those derived from whaling are largely based on small numbers of stranded animals or on small numbers of faecal samples from spatially separated individuals. For a large proportion of stranded animals, particularly those involved in single strandings, cause of death is unknown and is probably associated with disease. Subsequently, dietary assessments from such individuals may not reflect that of the healthy population. Mass-stranded animals however, are thought to be largely free of biases associated with disease (Aguilar *et al.* 1999). Faecal studies to date have been limited, as they can only ever report on partial samples. This is due to the identification of prey being restricted to hard part remains and of those, larger hard parts may sink before collection is possible, smaller parts may pass through meshed collecting devices and sampling is likely not to encompass all of the faeces passed by the animal. Differential digestion of species may further bias the results of faecal studies to particular species (Smith 1992)

An assessment of diet on a much smaller scale than before was made possible through the mass stranding of three groups of sperm whales on the west and north coasts of Tasmania in February 1998 (Chapter Two). Stomach samples from these animals provided a unique opportunity to compare diet of individuals between and among sperm whale groups and also across a range of age classes.

6.2. MATERIALS AND METHODS

Contents were collected from the stomachs of 36 sperm whales involved in two mass strandings (STR1: Ocean Beach, Strahan: n=15; STR2: Greens Pt. Beach, Marrawah: n=21). These were part of a series of three mass strandings of this species that occurred on the west and north coasts of Tasmania in 1998 (Chapter Two).

Samples were collected from whales post mortem 48 hours after the stranding was reported at STR1 and 24 hours after reporting at STR2. Full contents were often not collected due to an inability to access the whole stomach and time constraints, but in most cases, the complete contents of the second stomach (the primary area in which food

remains are found) were collected. In all cases the relative proportion of contents collected was estimated. Complete stomach contents were collected from 47 % of animals (sampling group A), contents were collected from the second stomach only in 50 % of all animals (sampling group B) and contents were collected from only part of the second stomach in 3 % of all animals (sampling group C). Contents were frozen at -20 °C on return to the University of Tasmania.

6.2.1. Sample analyses

Stomach samples were thawed, washed and sieved with a 0.5 mm sieve and then sorted into major taxonomic classes. Hard part remains were separated from soft parts and identified to the lowest taxon possible. In most cases this was to genus, but the state of digestion sometimes restricted this to order or class.

Identification of teleost and elasmobranch hard parts was carried out using the reference collections of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Marine Research laboratories, Hobart. Cephalopod beaks were separated from other cephalopod hard part remains and sorted into upper and lower beaks. The lower beaks were identified to the lowest taxonomic level possible using Voss (1969) and Clarke (1986) and a voucher collection of cephalopod beaks housed at the Australian Antarctic Division, Hobart. All cephalopod identifications were additionally verified against the cephalopod collections at the Museum of Victoria. Amongst the histioteuthids, where identification to species could not be made, beaks were separated into those of Type A and B (Clarke 1986), and distinctly different groups were assigned a number indicating an unidentified possible species group within the genus [*e.g.* *Histioteuthis* sp. Type B (1)].

Species were subsequently classified where possible in terms of ecotype, tissue composition (*i.e.* gelatinous or muscular) and vertical distribution using relevant literature on the biology, physiology and ecology of cephalopods (see Table 6.2 for a complete listing of references used). Ecotypes were defined as tropical (occurring around equatorial regions 0-20 °S), subtropical (known to occur north of the subtropical convergence at approximately 40 °S, but south of equatorial regions), subantarctic (known to occur south of the subtropical convergence) or Antarctic (known to occur south of the Antarctic Polar Front at approximately 55 °S).

Lower rostral lengths (LRLs) for squid and lower hood lengths (LHLs) for octopods were measured with vernier calipers to the nearest 0.1 mm. Allometric regression equations were used to estimate dorsal mantle length (DML) and wet body mass of individual cephalopods and octopods from LRLs and LHLs (Wolff 1984; Clarke 1986; Rodhouse *et al.* 1990; Lu and Williams 1994; Jackson *et al.* 1997; Lu and Ickeringill 2002). While many of these equations are based on too few specimens and therefore may not be accurate for some size classes, they provide a general guide to the size and weight of prey items (Clarke and Young 1998). Due to these limitations, all comparative analyses of prey size were conducted on LRLs or LHLs rather than on estimated DML or wet body mass.

6.2.2. Statistical analyses

Because of the importance of cephalopods in the diet of this species elsewhere and the predominance of cephalopods in the samples examined here, statistical analyses focused only on this prey group. Each individual whale was assigned an age based on counts of the number of growth layers in a tooth taken from that animal (Chapters Three and Four; Table 6.1) and then allocated to an age group. These corresponded to (1) juvenile or immature (female: ≤13 years; male: <19 years); (2) sexually mature but not physically mature (female: >13≤30 years; male: ≥19≤35 years) and (3) sexually and physically mature (female: >30 years; male: >35 years).

Because the relative proportion of stomach contents collected differed across samples, it was important to establish whether these differences biased the species diversity of samples. An analysis of co-variance (ANCOVA) tested whether there was any interaction between the sampling group and the total number of beaks (whether the slopes of these relationships differed) and whether the sampling group influenced the relationship between the number of species groups and the total number of beaks (whether the intercepts of these relationships differed). Data were log-transformed before analyses. As group C contained only one sample, only those data from groups A and B were tested.

Principal Components Analysis (PCA) was used to reduce the dimensionality of cephalopod species composition data (using percentage numerical abundance expressed as a percentage of the total number of beaks), while retaining as much of the variability present in the data. Discriminant Function Analysis (DFA) was then used to test if components derived from the PCA could be assigned to groups on the basis of stranding site, sex or age group using a Wilke's Lambda method at the 90 % significance level.

Backward stepwise analyses were used to determine the components that were responsible for any differences between groups tested and jackknife analysis was used to verify the accuracy of the DFA.

The percentage numerical abundance and abundance by percentage weight of cephalopod species from each ecotype and composition group in samples were compared between stranding sites, sex and age groups. Data were arcsine transformed and tested via a one-way nested ANOVA. Because of small sample sizes, immature animals were excluded from the dataset.

The mean LRLs of each cephalopod species contained in samples were compared between stranding sites and age groups using a one-way nested ANOVA. Data were tested for homogeneity and log-transformed if heterogeneous before conducting the nested ANOVA. Because of small sample sizes, immature animals and males were excluded from the dataset.

6.3. RESULTS

Stomach contents were dominated by intestinal nematodes and cephalopod beaks (Table 6.1), both of which occurred in all stomachs. While fragments of flesh occurred in 97 % of all samples, these were in varying stages of decomposition and at least some comprised of partially decomposed gastro-intestinal lining.

6.3.1. Non-cephalopod component of the diet

Non-cephalopod remains in the stomachs of sperm whales were dominated by intestinal nematodes, which were present in all samples and represented almost all of the undigested material present in each sample. Small numbers of fish bones and otoliths, crustacean exoskeletons, a gastropod and plastic debris were also present (Table 6.1).

Table 6.1: Composition of stomach content remains by frequency of occurrence (%F) in sperm whales from southern Australian waters.

Dietary group	Cephalopods	Fish	Nematodes	Invertebrates	Plastics	Unidentified flesh	Unidentified
All (n=36)	100.0	16.7	100.0	44.4	11.1	97.2	2.8
STR1 (n=15)	100.0	6.7	100.0	53.3	13.3	100.0	0.0
STR2 (n=21)	100.0	23.8	100.0	38.1	9.5	95.2	0.0
Age group 1 (n=2)	100.0	0.0	100.0	33.3	0.0	100.0	0.0
Age group 2 (n=14)	100.0	28.6	100.0	42.9	7.1	92.9	0.0
Age group 3 (n=15)	100.0	13.3	100.0	46.7	20.0	100.0	6.7
All Female (n=30)	100.0	10.0	100.0	46.7	13.3	96.7	3.3
Female Age group 1 (n=1)	100.0	0.0	100.0	0.0	0.0	100.0	0.0
Female Age group 2 (n=9)	100.0	11.1	100.0	55.6	11.1	88.9	0.0
Female Age group 3 (n=15)	100.0	13.3	100.0	46.7	20.0	100.0	6.7
All Male (n=6)	100.0	50.0	100.0	33.3	0.0	100.0	0.0
Male Age group 1 (n=1)	100.0	0.0	100.0	100.0	0.0	100.0	0.0
Male Age group 2 (n=5)	100.0	60.0	100.0	20.0	0.0	100.0	0.0

Identifiable fish remains were sparse, occurring in 16.7 % of all samples and were limited to hard parts. Two samples contained one highly eroded otolith each from the Family Myctophidae, one sample contained a number of partially digested cartilaginous parts from an unidentified elasmobranch and a vertebral section from an unidentified teleost. Four samples contained single vertebral segments from unidentified teleosts. Small sections of unidentifiable crustacean exoskeletons were present in 44.4 % of samples and one sample (2.8 % of all samples) contained one unidentified gastropod. Small pieces of plastic material were present in four samples (11.1 % of all samples), one of which also contained the top section of a plastic container (of approximately 2L in reconstructed volume). Three animals (0.75, 1.5 and 7 years) contained what appeared to be a milk-like substance present in their stomachs. Only the oldest of the three had hard part remains in the form of cephalopod beaks also present.

6.3.2. Cephalopod component of the diet

Cephalopod remains included beaks, partial gladii, complete and partial eyes and sucker rings and hooks. No buccal masses were identified in any of the samples. Remains of cephalopod pens were found in 66.7 % of all samples, whole or part cephalopod eyes were found in 94.4 % and cephalopod sucker rings and hooks were found in 11.1 %. Cephalopod beaks were present in all samples. A total of 101,883 cephalopod beaks (52,109 upper beaks, 49,774 lower beaks) were recovered from the 36 animals, representing species from three cephalopod orders, Teuthida, Octopoda and Vampyromorphida. Teuthids were represented by 48 species from 14 families, octopods by two species from two families and the Vampyromorphida by the one species *Vampyroteuthis infernalis* (Table 6.2). The average number of species present across all samples was 28.4 per sample (range: 4-45).

The proportion of stomach contents sampled did not have an effect on the relationship between total number of lower beaks and total number of species groups. The slopes of the relationship between species group number and total number of beaks of the two sampling groups were not significantly different ($F=1.4$, d.f.=1, $P=0.2$), nor were the intercepts of these relationships ($F<0.001$, d.f.=1, $P=0.9$). Subsequent analyses were therefore not restricted to those samples within individual sampling groups.

Table 6.2: Frequency of occurrence of cephalopod species in the stomach contents of sperm whales from Tasmania.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Haliphron atlanticus	11.1	6.7	14.3	0.0	21.4	0.0	10.0	0.0	22.2	0.0	16.7	0.0	20.0
Allopsidae	11.1	6.7	14.3	0.0	21.4	0.0	10.0	0.0	22.2	0.0	16.7	0.0	20.0
Ancistrocheirus lesueuri	69.4	73.3	66.7	50.0	71.4	60.0	70.0	0.0	77.8	60.0	66.7	100.0	60.0
Ancistrocheiridae	69.4	73.3	66.7	50.0	71.4	60.0	70.0	0.0	77.8	60.0	66.7	100.0	60.0
Architeuthis sp.	72.2	93.3	57.1	0.0	71.4	80.0	80.0	0.0	88.9	80.0	33.3	0.0	40.0
Architeuthidae	72.2	93.3	57.1	0.0	71.4	80.0	80.0	0.0	88.9	80.0	33.3	0.0	40.0
Japetella sp.	25.0	20.0	28.6	0.0	42.9	6.7	26.7	0.0	55.6	6.7	16.7	0.0	20.0
Bolitaneidae	25.0	20.0	28.6	0.0	42.9	6.7	26.7	0.0	55.6	6.7	16.7	0.0	20.0
Chiroteuthis joubini	63.9	73.3	57.1	50.0	57.1	60.0	73.3	100.0	77.8	62.5	16.7	0.0	20.0
Chiroteuthis veryani	88.9	86.7	90.5	50.0	92.9	86.7	90.0	0.0	100.0	86.7	83.3	100.0	80.0
Chiroteuthis sp.	22.2	20.0	23.8	50.0	35.7	6.7	23.3	0.0	55.6	6.7	16.7	100.0	0.0
Chiroteuthidae	91.7	93.3	90.5	100.0	92.9	86.7	93.3	100.0	100.0	86.7	83.3	0.0	80.0
Chtenopteryx sp.?	2.8	6.7	0.0	0.0	0.0	6.7	3.3	0.0	0.0	6.7	0.0	0.0	0.0
Chtenopterygidae	2.8	6.7	0.0	0.0	0.0	6.7	3.3	0.0	0.0	6.7	0.0	0.0	0.0
Cranchia scabra	36.1	33.3	38.1	0.0	35.7	33.3	43.3	0.0	55.6	33.3	0.0	0.0	0.0
Galiteuthis glacialis	91.7	93.3	90.5	100.0	85.7	93.3	96.7	100.0	100.0	93.3	66.7	100.0	60.0
Galiteuthis pacifica	8.3	13.3	4.8	0.0	21.4	0.0	10.0	0.0	33.3	0.0	0.0	0.0	0.0
Megalochranchia sp.	55.6	53.33	57.1	50.0	50.0	53.3	60.0	0.0	66.7	53.3	33.3	100.0	20.0
Mesonychoteuthis hamiltoni	86.1	80.0	90.5	50.0	100.0	73.3	83.3	0.0	100.0	73.3	100.0	100.0	100.0
Taonius pavo	77.8	86.7	71.4	50.0	78.6	73.3	80.0	0.0	88.9	73.3	66.7	100.0	60.0
Teuthowenia pellucida	80.6	93.3	71.4	50.0	71.4	86.7	86.7	0.0	88.9	86.7	50.0	100.0	40.0
Cranchiidae	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 6.2 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Cycloteuthis akimushkini	2.8	6.7	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0
Discoteuthis discus	11.1	20.0	4.7	0.0	14.3	6.7	10.0	0.0	11.1	6.7	16.7	0.0	20.0
Cycloteuthidae	13.9	26.7	4.8	0.0	14.3	6.7	13.3	0.0	11.1	6.7	16.7	0.0	20.0
Gonatus antarcticus	47.2	60.0	38.1	0.0	42.9	40.0	53.3	0.0	55.6	40.0	16.7	0.0	20.0
Gonatidae	47.2	60.0	38.1	0.0	42.9	40.0	53.3	0.0	55.6	40.0	16.7	0.0	20.0
Histioteuthis A1	5.6	13.3	0.0	0.0	0.0	6.7	6.7	0.0	0.0	6.7	0.0	0.0	0.0
Histioteuthis macrohista	55.6	80.0	38.1	50.0	64.3	46.7	63.3	100.0	88.9	46.7	16.7	0.0	20.0
Histioteuthis melaegroteuthis	52.8	66.7	42.9	0.0	57.1	46.7	60.0	0.0	77.8	46.7	16.7	0.0	20.0
Histioteuthis bonnelli	69.4	73.3	66.7	50.0	71.4	60.0	73.3	0.0	88.9	60.0	50.0	100.0	40.0
Histioteuthis celetaria pacifica	22.2	20.0	23.8	0.0	21.4	13.3	20.0	0.0	11.1	13.3	33.3	0.0	40.0
Histioteuthis miranda	63.9	80.0	52.4	50.0	50.0	66.7	70.0	0.0	66.7	66.7	33.3	100.0	20.0
Histioteuthis hoylei	55.6	66.7	47.6	50.0	42.9	53.3	60.0	0.0	55.6	53.3	33.3	100.0	20.0
Histioteuthis sp. Type A (1)	25.0	33.3	19.0	0.0	35.7	20.0	30.0	0.0	55.6	20.0	0.0	0.0	0.0
Histioteuthis B1	63.9	66.7	61.9	0.0	78.6	46.7	66.7	0.0	88.9	46.7	50.0	0.0	60.0
Histioteuthis eltaninae	63.9	66.7	61.9	0.0	71.4	60.0	70.0	0.0	88.9	60.0	33.3	0.0	40.0
Histioteuthis B2	94.4	93.3	95.2	50.0	100.0	93.3	93.3	0.0	100.0	93.3	100.0	100.0	100.0
Histioteuthis reversa	27.8	6.7	42.9	50.0	42.9	13.3	23.3	0.0	44.4	13.3	50.0	100.0	40.0
Histioteuthis atlantica	91.7	86.7	95.2	50.0	100.0	86.7	90.0	0.0	100.0	86.7	100.0	100.0	100.0

Table 6.2 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Histioteuthis B4	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Histioteuthis sp. Type B(1)	13.9	13.3	14.3	0.0	7.1	13.3	16.7	0.0	11.1	13.3	0.0	0.0	0.0
Histioteuthis sp. Type B(2)	77.8	80.0	76.2	0.0	85.7	73.3	80.0	0.0	88.9	73.3	66.7	0.0	80.0
Histioteuthidae	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Lepidoteuthis grimaldi	97.2	100.0	95.2	100.0	100.0	93.3	96.7	100.0	100.0	93.3	100.0	100.0	100.0
Lepidoteuthidae	97.2	100.0	95.2	100.0	100.0	93.3	96.7	100.0	100.0	93.3	100.0	100.0	100.0
Idioteuthis cordiformis	75.0	86.7	76.2	50.0	71.4	73.3	76.7	0.0	77.8	73.3	66.7	100.0	60.0
Mastigoteuthis psychrophile	5.6	6.7	4.8	0.0	14.3	0.0	6.7	0.0	22.2	0.0	0.0	0.0	0.0
Mastigoteuthis sp.	27.8	26.7	28.6	0.0	28.6	20.0	30.0	0.0	33.3	20.0	16.7	0.0	20.0
Mastigoteuthidae	75.0	86.7	66.7	50.0	71.4	73.3	76.7	0.0	77.8	73.3	66.7	100.0	60.0
Octopoteuthis rugosa	80.6	86.7	76.2	0.0	85.7	80.0	86.7	0.0	100.0	80.0	50.0	0.0	60.0
Taningia danae	72.2	86.7	61.9	0.0	85.7	60.0	76.7	0.0	100.0	60.0	50.0	0.0	60.0
Octopoteuthidae	88.9	93.3	85.7	0.0	100.0	86.7	90.0	0.0	100.0	86.7	66.7	0.0	100.0
Nototodarus gouldi	72.2	66.7	76.2	50.0	78.6	60.0	73.3	0.0	88.9	60.0	66.7	100.0	60.0
Ommastrephes bartrami	41.7	60.0	28.6	0.0	42.9	33.3	50.0	0.0	66.7	33.3	0.0	0.0	0.0
Todarodes fillapovae	88.9	86.7	90.5	100.0	92.9	80.0	90.0	100.0	100.0	80.0	83.3	100.0	80.0
Ommastrephidae	91.7	86.7	95.2	100.0	100.0	80.0	90.0	100.0	100.0	80.0	100.0	100.0	100.0
Kondakovia longimana	86.1	80.0	90.5	50.0	85.7	86.7	86.7	0.0	88.9	86.7	83.3	100.0	80.0
Moroteuthis 'A'/ingens	66.7	86.7	52.4	0.0	78.6	66.7	66.7	0.0	77.8	66.7	66.7	0.0	80.0

Table 6.2 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Moroteuthis knipovitchi	63.9	80.0	52.4	0.0	64.2	60.0	73.3	0.0	88.9	60.0	16.7	0.0	20.0
Moroteuthis lonnbergii	63.9	60.0	66.7	0.0	71.4	53.3	60.0	0.0	55.6	53.3	83.3	0.0	100.0
Moroteuthis robsoni	91.7	86.7	95.2	50.0	100.0	86.7	90.0	0.0	100.0	86.7	100.0	100.0	100.0
Onychoteuthidae	94.4	93.3	95.2	50.0	100.0	93.3	93.3	0.0	100.0	93.3	100.0	100.0	100.0
Pholidoteuthis adami	13.9	13.3	14.3	0.0	28.6	6.7	16.7	0.0	44.4	6.7	0.0	0.0	0.0
Pholidoteuthis boschmai	91.7	86.7	95.2	0.0	100.0	93.3	93.3	0.0	100.0	93.3	83.3	0.0	100.0
Pholidoteuthidae	91.7	86.7	95.2	0.0	100.0	93.3	93.3	0.0	100.0	93.3	83.3	0.0	100.0
Vampyroteuthis infernalis	27.8	46.7	14.3	0.0	35.7	20.0	30.0	0.0	44.4	20.0	16.7	0.0	20.0
Vampyroteuthidae	27.8	46.7	14.3	0.0	35.7	20.0	30.0	0.0	44.4	20.0	16.7	0.0	20.0
Unidentified	72.2	80.0	66.7	0.0	78.6	66.7	76.7	0.0	88.9	66.7	50.0	0.0	60.0

6.3.2.1. Cephalopod species composition

Members of the Histioteuthidae family dominated samples by frequency of occurrence and by number. The species *Histioteuthis* B4 was the most numerous (7,127 lower beaks, 14.2 % numerical abundance; Tables 6.2 and 6.3). Other important species both by frequency of occurrence and numerically included *Histioteuthis* B2 (6,202, 12.5 %N), *H. atlantica* (4,739, 9.5 %N), *Lepidoteuthis grimaldi* (4,632, 9.3 %N) and *H. bonnelli* (2,782, 5.6 %N). Of the total 51 species, 25 accounted for over 92 % of numerical abundance.

Estimated fresh wet mass for all species identified were not available due to a lack of regression equations for three species (*D. discus*, *Japatella* sp. and *L. grimaldi*), therefore limiting interpretation of the contribution of individual species to overall mass. Of the estimated fresh wet mass calculated, the Histioteuthids collectively were also important by weight contributing 14.3 % to the total estimated mass, with the family Onychoteuthidae contributing the largest proportion by weight (36.5%; Table 6.4). Of the total 51 species, 13 accounted for over 90 % of the estimated total wet weight. *Moroteuthis robsoni* (32.5 %), *Architeuthis* sp. (13.6 %), *Pholidoteuthis boschmai* (11.4 %), *Todarodes filappovae* (6.6 %) and *Taningia danae* (5.0 %) were important species in terms of the estimated wet mass.

6.3.2.2. Cephalopod species composition with respect to stranding group, sex and age

Principal Component Analysis on species composition data produced the groupings illustrated in Figure 6.1. There was a high degree of variability in the data, with the first five components describing only 45.3 % of the total variance. Fifteen components were required to describe 82.6 % of the total variance. Despite the high variability observed in the data with PCA, significant differences in cephalopod species composition between stranding sites (Wilke's Lambda=0.4, d.f.=5, $P<0.001$) and sexes (Wilke's Lambda= 0.1, d.f=9, $P<0.001$), but not age groups (Wilke's Lambda=0.95, d.f.=3, $P=0.7$) were demonstrated with DFA. Five species contributed to the differences observed between stranding sites (Table 6.5) with 94.4 % of original cases and 88.9 % of cross validated cases correctly classified on the basis of these five species with backward stepwise analysis. Nine species contributed to the differences observed between sexes (Table 6.5) with 100% of original cases and 97.2 % of cross-validated cases correctly classified on the basis of the nine species with backward stepwise analysis.

Table 6.3: Abundance by number (expressed as a percentage of the total number of beaks) of cephalopod species in the stomach contents of sperm whales from Tasmania.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Haliphron atlanticus	0.03	0.01	0.04	0.0	0.05	0.0	0.01	0.0	0.04	0.0	0.2	0.0	0.2
Allopsidae	0.03	0.01	0.04	0.0	0.05	0.0	0.01	0.0	0.04	0.0	0.2	0.0	0.2
Ancistrocheirus lesueuri	2.1	1.9	2.5	2.4	2.1	1.8	2.2	0.0	2.3	1.8	0.9	3.0	0.8
Ancistrocheiridae	2.1	1.9	2.5	2.4	2.1	1.8	2.2	0.0	2.3	1.8	0.9	3.0	0.8
Architeuthis sp.	1.0	1.6	0.3	0.0	0.6	1.1	1.0	0.0	0.6	1.1	0.3	0.0	0.3
Architeuthidae	1.0	1.6	0.3	0.0	0.6	1.1	1.0	0.0	0.6	1.1	0.3	0.0	0.3
Japetella sp.	0.1	0.03	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1
Bolitaneidae	0.1	0.03	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1
Chiroteuthis joubini	0.7	0.8	0.5	1.2	0.4	0.6	0.7	5.9	0.5	0.6	0.1	0.0	0.1
Chiroteuthis veryani	2.8	2.6	3.0	1.2	3.0	2.6	2.9	0.0	3.1	2.6	1.7	1.5	1.7
Chiroteuthis sp.	0.1	0.01	0.1	1.2	0.2	0.01	0.1	0.0	0.2	0.01	0.1	1.5	0.0
Chiroteuthidae	3.5	3.5	3.6	3.5	3.6	3.2	3.6	5.9	3.7	3.2	1.9	3.0	1.9
Chtenopteryx sp.?	0.002	0.004	0.0	0.0	0.0	0.01	0.002	0.0	0.0	0.01	0.0	0.0	0.0
Chtenopterygidae	0.002	0.004	0.0	0.0	0.0	0.01	0.002	0.0	0.0	0.01	0.0	0.0	0.0
Cranchia scabra	0.1	0.1	0.2	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0
Galiteuthis glacialis	2.7	1.6	4.0	4.8	2.8	2.6	2.7	5.9	3.0	2.6	0.8	4.5	0.7
Galiteuthis pacifica	0.01	0.01	0.004	0.0	0.02	0.0	0.01	0.0	0.03	0.0	0.0	0.0	0.0
Megalochranchia sp.	1.2	0.8	1.6	1.2	1.3	0.2	1.2	0.0	1.4	0.2	0.3	1.5	0.2
Mesonychoteuthis hamiltoni	1.6	1.0	2.4	2.4	1.7	5.1	1.5	0.0	1.3	5.1	5.0	3.0	5.1
Taonius pavo	2.0	2.8	1.2	1.2	2.0	0.9	2.1	0.0	2.1	0.9	0.9	1.5	0.9
Teuthowenia pellucida	1.8	1.8	1.7	2.4	1.7	0.5	1.8	0.0	1.8	0.5	0.6	3.0	0.5

Table 6.3 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Cranchiidae	9.4	8.0	11.1	11.9	9.6	9.3	9.5	5.9	9.8	9.3	7.6	13.4	7.4
Cycloteuthis akimushkini	0.002	0.004	0.0	0.0	0.0	0.0	0.002	0.0	0.0	0.0	0.0	0.0	0.0
Discoteuthis discus	0.03	0.1	0.004	0.0	0.03	0.01	0.03	0.0	0.03	0.01	0.1	0.0	0.1
Cycloteuthidae	0.03	0.1	0.004	0.0	0.03	0.004	0.03	0.0	0.03	0.004	0.1	0.0	0.1
Gonatus antarcticus	0.1	0.2	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1
Gonatidae	0.1	0.2	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1
Histioteuthis A1	0.1	0.3	0.0	0.0	0.0	0.3	0.2	0.0	0.0	0.3	0.0	0.0	0.0
Histioteuthis macrohista	0.6	0.3	1.1	1.2	0.5	1.0	0.7	5.9	0.5	1.0	0.1	0.0	0.1
Histioteuthis melaegroteuthis	0.6	0.4	1.0	0.0	0.6	0.6	0.7	0.0	0.6	0.6	0.4	0.0	0.4
Histioteuthis bonnelli	5.6	3.8	7.8	10.7	5.4	5.9	5.8	0.0	5.9	5.9	1.3	13.4	0.8
Histioteuthis celetaria pacifica	0.03	0.03	0.04	0.0	0.1	0.01	0.03	0.0	0.03	0.01	0.2	0.0	0.2
Histioteuthis miranda	1.1	0.7	1.5	2.4	1.1	0.9	1.1	0.0	1.2	0.9	0.5	3.0	0.4
Histioteuthis hoylei	2.1	1.6	2.7	2.4	2.4	1.6	2.1	0.0	2.5	1.6	1.6	3.0	1.5
Histioteuthis sp. Type A (1)	0.2	0.3	0.1	0.0	0.3	0.1	0.2	0.0	0.3	0.1	0.0	0.0	0.0
Histioteuthis B1	2.5	4.2	0.5	0.0	0.9	4.0	2.6	0.0	1.0	4.0	0.7	0.0	0.7
Histioteuthis eltaninae	3.6	2.1	5.5	0.0	3.4	4.1	3.7	0.0	3.7	4.1	1.3	0.0	1.3
Histioteuthis B2	12.5	13.8	10.9	1.2	13.4	13.0	12.8	0.0	14.3	13.0	4.9	1.5	5.1
Histioteuthis reversa	0.8	0.5	1.1	6.0	1.3	0.4	0.7	0.0	1.3	0.4	1.7	7.5	1.5

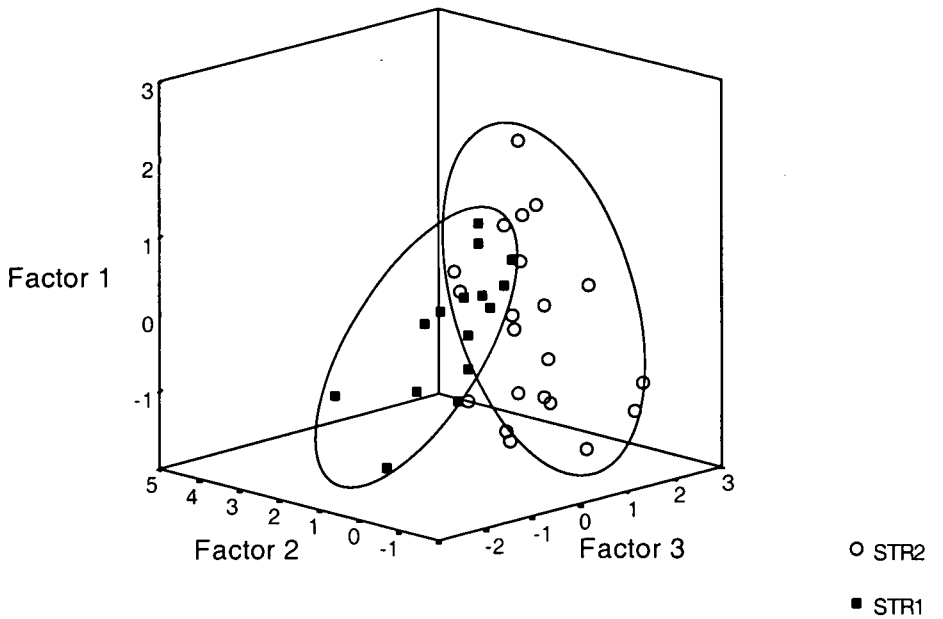
Table 6.3 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Histioteuthis atlantica	9.5	10.9	7.9	3.6	9.1	11.0	9.5	0.0	8.9	11.0	11.0	4.5	11.3
Histioteuthis B4	14.3	19.8	7.7	25.0	13.2	15.5	14.1	64.7	12.6	15.5	18.9	14.9	19.1
Histioteuthis sp. Type B(1)	0.5	0.5	0.4	0.0	0.4	0.4	0.5	0.0	0.4	0.4	0.0	0.0	0.0
Histioteuthis sp. Type B(2)	0.6	0.6	0.6	0.0	0.6	1.2	0.6	0.0	0.6	1.2	1.1	0.0	1.2
Histioteuthidae	54.7	60.0	48.7	52.4	52.8	59.2	55.1	70.6	53.8	59.2	43.6	47.8	43.4
Lepidoteuthis grimaldi	9.3	7.8	11.1	8.3	10.7	16.1	9.1	5.9	10.1	16.1	15.9	9.0	16.1
Lepidoteuthidae	9.3	7.8	11.1	8.3	10.7	7.5	9.1	5.9	10.1	7.5	15.9	9.0	16.1
Idioteuthis cordiformis	0.9	0.6	1.2	1.2	0.9	1.2	0.9	0.0	0.9	1.2	1.2	1.5	1.2
Mastigoteuthis psychrophile	0.01	0.01	0.004	0.0	0.01	0.0	0.01	0.0	0.02	0.0	0.0	0.0	0.0
Mastigoteuthis sp.	0.1	0.03	0.1	0.0	0.03	0.1	0.1	0.0	0.03	0.1	0.1	0.0	0.1
Mastigoteuthidae	1.0	0.7	1.3	1.2	0.9	0.9	0.9	0.0	0.9	0.9	1.3	1.5	1.3
Octopoteuthis rugosa	2.0	2.1	1.9	0.0	2.1	3.2	2.0	0.0	2.0	3.2	3.1	0.0	3.2
Taningia danae	0.6	0.9	0.3	0.0	0.6	0.6	0.6	0.0	0.6	0.6	0.8	0.0	5.7
Octopoteuthidae	2.7	3.0	2.2	0.0	2.7	2.6	2.6	0.0	2.6	2.6	3.7	0.0	3.9
Nototodarus gouldi	0.7	0.8	0.6	2.4	0.6	1.4	0.7	0.0	0.5	1.4	1.5	3.0	1.4
Ommastrephes bartrami	0.1	0.1	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0
Todarodes fillapovae	2.2	2.4	2.1	6.0	2.3	1.2	2.3	11.8	2.4	1.2	1.3	0.0	1.2
Ommastrephidae	3.9	4.3	3.5	8.3	3.8	3.6	3.9	11.8	3.8	3.6	3.5	7.5	3.3
Kondakovia longimana	1.3	0.9	1.7	1.2	0.9	1.2	1.3	0.0	0.8	1.2	1.2	1.5	1.2

Table 6.3 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Moroteuthis 'A'lingens	0.3	0.3	0.2	0.0	0.2	0.8	0.2	0.0	0.2	0.8	0.8	0.0	0.8
Moroteuthis knipovitchi	0.7	0.6	0.7	0.0	0.5	0.1	0.7	0.0	0.5	0.1	0.1	0.0	0.1
Moroteuthis lonnbergii	0.4	0.3	0.5	0.0	0.4	0.7	0.4	0.0	0.4	0.7	0.7	0.0	0.7
Moroteuthis robsoni	2.7	1.9	3.8	10.7	3.1	8.9	2.5	0.0	2.6	8.9	9.0	13.4	8.9
Onychoteuthidae	5.3	4.0	6.9	11.9	5.2	5.0	5.1	0.0	4.5	5.0	11.8	14.9	11.7
Pholidoteuthis adami	0.03	0.03	0.02	0.0	0.1	0.0	0.03	0.0	0.1	0.0	0.0	0.0	0.0
Pholidoteuthis boschmai	4.6	3.4	6.2	0.0	5.3	5.7	4.6	0.0	5.3	5.7	5.5	0.0	5.7
Pholidoteuthidae	4.7	3.4	6.2	0.0	5.4	4.4	4.6	0.0	5.4	4.4	5.5	0.0	5.7
Vampyroteuthis infernalis	0.04	0.1	0.02	0.0	0.1	0.1	0.04	0.0	0.1	0.1	0.1	0.0	0.1
Vampyroteuthidae	0.04	0.1	0.02	0.0	0.1	0.1	0.04	0.0	0.1	0.1	0.1	0.0	0.1
Unidentified	2.1	1.9	2.4	0.0	2.4	1.2	2.1	3.8	2.2	1.2	3.8	0.0	4.0

A.



B.

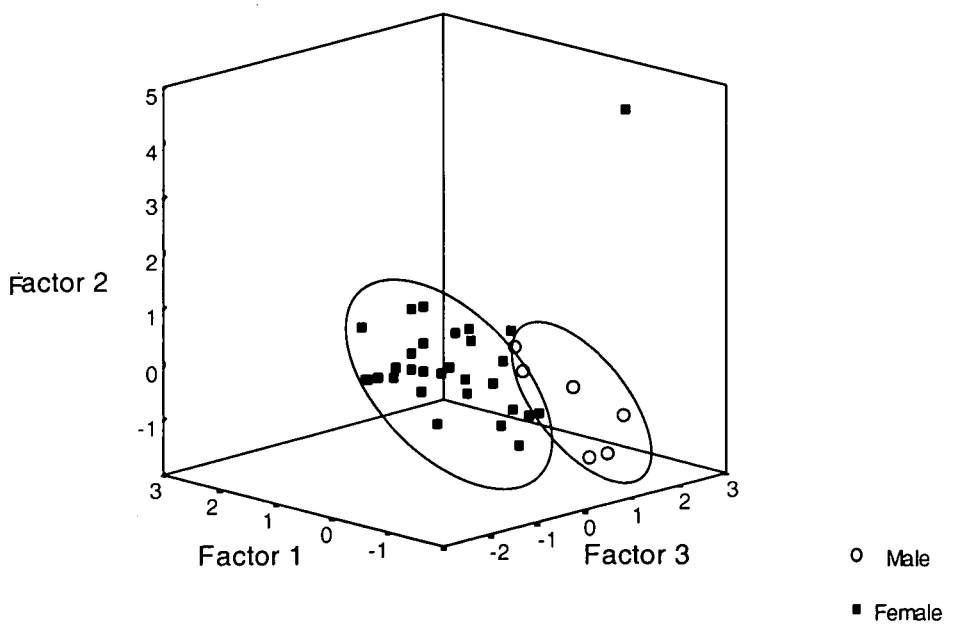


Figure 6.1: Three-dimensional plot of the results of principal component analysis conducted on the cephalopod species composition of samples (a) between STR1 and STR2 and (b) between males and females.

Overall, diet samples were dominated by subtropical and muscular species (Table 6.6; Figures 6.2 and 6.3). The numerical abundance of species in each ecotype group was significantly different between stranding groups ($F_{1,6}$=1.6, P=0.02) and sexes ($F_{1,6}$=3.6, P=0.001), but not between age groups ($F_{1,6}$=0.9, P=0.5). Individuals from STR1 contained higher abundances of subtropical species, while those from STR2 contained higher abundances of tropical/subtropical, subantarctic and Antarctic species. Females contained higher abundances of subtropical, subantarctic and Antarctic species, while males contained higher abundances of tropical/subtropical and subantarctic/Antarctic species. However, when comparing the abundance of species in each ecotype on the basis of percentage weight, no significant differences were observed between stranding sites ($F_{1,6}$=1.6, P=0.2), sexes ($F_{1,6}$=1.3, P=0.2) or age groups ($F_{1,6}$=0.3, P=0.9). The abundance of muscular and gelatinous cephalopod species was not significantly different between stranding sites, sexes or age groups both in terms of numerical abundance (site: $F_{1,1}$=0.001, P=0.9; sex: $F_{1,1}$=0.01, P=0.9; age: $F_{1,1}$=0.3, P=0.6) or percentage weight abundance (site: $F_{1,1}$=0.1, P=0.7; sex: $F_{1,1}$=0.04, P=0.8; age: $F_{1,1}$=0.1, P=0.7).

6.3.2.3. Size of cephalopods

The size of cephalopod prey varied considerably. Lower rostral lengths of all species ranged from 1.3-40.7 mm (Table 6.7) and calculated DMLs from all species ranged from 10.7-2,640.7 mm with a mean size of prey consumed of 233.7±215.7 mm (Table 6.8). Only *Architeuthis* sp, *L. grimaldi*, *Mesonychoteuthis hamiltoni*, *M. robsoni* and *T. danae* were represented by individuals calculated to have had DMLs larger than 1,000 mm. Cephalopods larger than 1,000 mm comprised only 0.6 % of all cephalopods present in the samples, while those less than 300 mm comprised 73.5 % (Figure 6.4). Estimated wet masses also varied considerably, ranging from 2.7-110,233.1 gm (Table 6.9) with a mean estimated wet mass of 828.3±3,073.6 gm. Twenty species were represented by individuals greater than 1,000 gm estimated wet mass and those larger than 1,000 gm comprised 78.6 % of the estimated total wet mass (Figure 6.5).

Table 6.4: Percentage of total mass of cephalopod species in the stomach contents of sperm whales from Tasmania.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Haliphron atlanticus	0.04	0.03	0.04	0.0	0.1	0.0	0.04	0.0	0.1	0.0	0.04	0.0	0.04
Allopsidae	0.04	0.03	0.04	0.0	0.1	0.0	0.04	0.0	0.1	0.0	0.04	0.0	0.04
Ancistrocheirus lesueuri	3.8	3.2	4.5	2.7	3.1	3.3	4.1	0.0	3.7	3.3	0.6	2.8	0.5
Ancistrocheiridae	3.8	3.2	4.5	2.7	3.1	3.3	4.1	0.0	3.7	3.3	0.6	2.8	0.5
Architeuthis sp.	13.6	22.5	3.3	0.0	8.4	15.0	14.4	0.0	9.6	15.0	3.1	0.0	3.2
Architeuthidae	13.6	22.5	3.3	0.0	8.4	15.0	14.4	0.0	9.6	15.0	3.1	0.0	3.2
Japetella sp.	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Bolitaneidae	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Chiroteuthis joubini	0.2	0.2	0.1	0.1	0.1	0.2	0.2	1.0	0.1	0.2	0.03	0.0	0.03
Chiroteuthis veryani	0.6	0.5	0.7	0.5	0.6	0.6	0.6	0.0	0.7	0.6	0.2	0.5	0.2
Chiroteuthis sp.	0.01	0.0	0.02	0.5	0.02	0.0	0.01	0.0	0.03	0.0	0.02	0.5	0.0
Chiroteuthidae	0.8	0.7	0.9	1.0	0.7	0.8	0.8	1.0	0.8	0.8	0.3	1.0	0.2
Chtenopteryx sp.?	0.0001	0.0001	0.0	0.0	0.0	0.0001	0.0001	0.0	0.0	0.0001	0.0	0.0	0.0
Chtenopterygidae	0.0001	0.0001	0.0	0.0	0.0	0.0001	0.0001	0.0	0.0	0.0001	0.0	0.0	0.0
Cranchia scabra	0.01	0.003	0.01	0.0	0.01	0.01	0.01	0.0	0.01	0.01	0.0	0.0	0.0
Galiteuthis glacialis	0.3	0.2	0.4	0.2	0.3	0.3	0.3	0.6	0.4	0.3	0.1	0.2	0.1
Galiteuthis pacifica	0.001	0.001	0.0003	0.0	0.002	0.0	0.001	0.0	0.002	0.0	0.0	0.0	0.0
Megalochranchia sp.	0.2	0.1	0.3	0.0	0.3	0.2	0.2	0.0	0.3	0.2	0.0	0.0	0.0
Mesonychoteuthis hamiltoni	2.1	1.2	3.1	0.9	2.4	2.1	1.8	0.0	1.8	2.1	5.3	5.4	1.0
Taonius pavo	0.7	1.0	0.4	0.3	0.7	0.7	0.8	0.0	0.9	0.7	0.2	0.3	0.2
Teuthowenia pellucida	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.0	0.6	0.6	0.1	0.7	0.1
Cranchiidae	3.9	3.1	4.7	2.0	4.2	3.9	3.7	0.6	3.8	3.9	5.6	2.1	5.8

Table 6.4 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Cycloteuthis akimushkini	0.004	0.001	0.01	0.0	0.01	0.0	0.004	0.0	0.01	0.0	0.0	0.0	0.0
Discoteuthis discus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Cycloteuthidae	0.004	0.001	0.01	0.0	0.01	0.0	0.004	0.0	0.01	0.0	0.0	0.0	0.0
Gonatus antarcticus	0.1	0.1	0.03	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.02	0.0	0.02
Gonatidae	0.1	0.1	0.03	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.02	0.0	0.02
Histioteuthis A1	0.04	0.1	0.0	0.0	0.0	0.1	0.04	0.0	0.0	0.1	0.0	0.0	0.0
Histioteuthis macrohista	0.1	0.02	0.2	0.1	0.1	0.2	0.1	1.3	0.1	0.2	0.002	0.0	0.002
Histioteuthis melaegroteuthis	0.1	0.03	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.02	0.0	0.02
Histioteuthis bonnelli	1.5	1.1	1.9	1.6	1.5	1.5	1.6	0.0	1.8	1.5	0.2	1.7	0.1
Histioteuthis celetaria pacifica	0.01	0.01	0.01	0.0	0.02	0.01	0.01	0.0	0.01	0.01	0.1	0.0	0.1
Histioteuthis miranda	0.9	0.6	1.2	1.0	0.9	0.7	0.9	0.0	1.1	0.7	0.2	1.1	0.2
Histioteuthis hoylei	0.9	0.8	1.1	0.7	1.2	0.6	1.0	0.0	1.4	0.6	0.4	0.8	0.4
Histioteuthis sp. Type A (1)	0.1	0.1	0.03	0.0	0.1	0.03	0.1	0.0	0.1	0.03	0.0	0.0	0.0
Histioteuthis B1	0.7	1.2	0.1	0.0	0.3	1.1	0.8	0.0	0.3	1.1	0.1	0.0	0.1
Histioteuthis eltaninae	0.7	0.4	1.0	0.0	0.7	0.8	0.8	0.0	0.8	0.8	0.1	0.0	0.1
Histioteuthis B2	3.0	3.6	2.3	0.2	3.5	3.0	3.2	0.0	4.1	3.0	0.7	0.2	0.7
Histioteuthis reversa	0.1	0.1	0.2	0.7	0.3	0.1	0.1	0.0	0.3	0.1	0.2	0.8	0.1
Histioteuthis atlantica	2.3	2.7	1.8	0.5	2.4	2.6	2.4	0.0	2.6	2.6	1.4	0.5	1.4

Table 6.4 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Histioteuthis B4	3.6	5.2	1.9	3.5	3.5	3.8	3.7	27.4	3.7	3.8	2.5	1.9	2.5
Histioteuthis sp. Type B(1)	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0
Histioteuthis sp. Type B(2)	0.2	0.2	0.1	0.0	0.2	0.1	0.2	0.0	0.2	0.1	0.2	0.0	0.2
Histioteuthidae	14.3	16.1	12.2	8.3	14.7	14.7	15.0	28.7	16.7	14.7	6.0	7.0	5.9
Lepidoteuthis grimaldi	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Lepidoteuthidae	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Idioteuthis cordiformis	0.4	0.2	0.5	0.4	0.4	0.3	0.4	0.0	0.4	0.3	0.3	0.4	0.3
Mastigoteuthis psychrophile	0.0002	0.0002	0.0002	0.0	0.001	0.0	0.0002	0.0	0.001	0.0	0.0	0.0	0.0
Mastigoteuthis sp.	0.01	0.01	0.01	0.0	0.01	0.01	0.01	0.0	0.01	0.01	0.01	0.0	0.01
Mastigoteuthidae	0.4	0.2	0.5	0.4	0.4	0.3	0.4	0.0	0.4	0.3	0.3	0.4	0.3
Octopoteuthis rugosa	0.7	0.8	0.5	0.0	0.7	0.6	0.7	0.0	0.7	0.6	0.5	0.0	0.5
Taningia danae	5.0	7.0	2.8	0.0	4.3	6.3	5.2	0.0	4.6	6.3	2.8	0.0	2.9
Octopoteuthidae	5.6	7.7	3.3	0.0	5.0	7.0	5.8	0.0	5.4	7.0	3.3	0.0	3.4
Nototodarus gouldi	2.6	3.3	1.9	1.6	2.0	2.4	2.6	0.0	1.9	2.4	2.7	1.7	2.8
Ommastrephes bartrami	0.4	0.5	0.3	0.0	0.5	0.3	0.4	0.0	0.6	0.3	0.0	0.0	0.0
Todarodes fillapovae	6.6	7.7	5.4	10.1	7.0	5.8	7.0	69.8	8.1	5.8	2.0	6.3	1.8
Ommastrephidae	9.6	11.4	7.6	11.7	9.4	8.5	10.0	69.8	10.5	8.5	4.7	8.0	4.6
Kondakovia longimana	2.7	1.3	4.3	3.4	2.4	2.6	2.7	0.0	2.4	2.6	2.5	3.6	2.4
Moroteuthis 'A'/ingens	0.7	0.9	0.5	0.9	2.4	2.1	0.7	0.0	1.7	2.1	1.2	1.0	5.4

Table 6.4 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Moroteuthis knipovitchi	0.3	0.2	0.3	0.0	0.2	0.3	0.3	0.0	0.2	0.3	0.02	0.0	0.02
Moroteuthis lonnbergii	0.4	0.4	0.4	0.0	0.3	0.3	0.4	0.0	0.3	0.3	0.3	0.0	0.3
Moroteuthis robsoni	32.5	23.9	42.4	70.5	36.6	31.8	30.0	0.0	30.6	31.8	64.0	75.1	63.5
Onychoteuthidae	36.5	26.7	47.8	73.9	40.1	35.8	34.0	0.0	34.0	35.8	67.9	78.7	67.5
Pholidoteuthis adami	0.01	0.01	0.01	0.0	0.02	0.001	0.01	0.0	0.03	0.001	0.0	0.0	0.0
Pholidoteuthis boschmai	11.4	8.2	15.1	0.0	13.7	10.6	11.7	0.0	14.8	10.6	8.3	0.0	8.7
Pholidoteuthidae	11.4	8.2	15.1	0.0	13.7	10.6	11.7	0.0	14.9	10.6	8.3	0.0	8.7
Vampyroteuthis infernalis	0.03	0.03	0.02	0.0	0.1	0.01	0.02	0.0	0.1	0.01	0.1	0.0	0.1
Vampyroteuthidae	0.03	0.03	0.02	0.0	0.1	0.01	0.02	0.0	0.1	0.01	0.1	0.0	0.1

n/a: not available.

6.3.2.4. Size of cephalopods with respect to stranding group and age

Mean LRLs of 20 cephalopod species present in samples differed significantly between stranding sites and mean LRLs of 17 species differed significantly between the age groups two and three (Table 6.10). Individuals from STR1 contained larger beaks of *Architeuthis* sp., *L. grimaldi*, *Moroteuthis lonnbergii*, the Ommastrephids and *O. rugosa* while those from STR2 contained larger beaks of *Chiroteuthis v. veryani*, the type A Histioteuthids, *Idioteuthis cordiformis*, *M. hamiltoni*, *M. robsoni*, and *T. pavo*. Individuals from age group two contained larger beaks of *Galiteuthis glacialis*, most Histioteuthids and *Kondakovia longimana*, while those from age group three contained larger beaks of *Cranchia scabra*, *Teuthowenia pellucida*, *H. macrohista*, *Histioteuthis* B1, *L. grimaldi* and the three *Moroteuthis* species (Table 6.10).

Table 6.5: Percentage abundance of cephalopod species identified by discriminant function analysis contributing to cephalopod species composition differences between sperm whales from STR1 and STR2 and between male and female sperm whales.

	Site			Sex	
Species	STR1	STR2	Species	Female	Male
Megalocranchia sp.	0.8	1.6	*Haliphron atlanticus*	0.01	0.2
Ommastrephes bartrami	0.1	0.1	*Chiroteuthis veryani*	2.9	1.5
Moroteuthis robsoni	1.9	3.8	*Mesonychoteuthis hamiltoni*	1.5	5.0
Pholidoteuthis boschmai	3.4	6.2	*Mastigoteuthis psychrophile*	0.01	0.0
Vampyroteuthis infernalis	0.1	0.02	*Octopoteuthis rugosa*	2.0	3.1
			Nototodarus gouldi	0.7	1.5
			Kondokovia longimana	1.3	1.5
			Moroteuthis knipovitchi	0.7	0.1
			Moroteuthis robsoni	2.5	9.0

Table 6.6: Distribution, composition, and maximum recorded size of cephalopod species identified from the stomach contents of sperm whales from Tasmania.

Species	Ecotype	Tissue composition	Depth distribution (m)	Maximum GL/ML/TL (mm)	Species	Ecotype	Tissue composition	Depth distribution (m)	Maximum GL/ML/TL (mm)
Haliphron atlanticus	st/sa	g	0-3180	108ML	*Histioteuthis* B1	st	n/a	n/a	n/a
Ancistrocheirus lesueuri	t/st	g	80-2000	390ML	*Histioteuthis eltaninae*	sa	g	30-2890	105ML
Architeuthis sp.	st	m	295-1100	4000ML	*Histioteuthis* B2	st	n/a	n/a	n/a
Japetella sp.	t/st	g	0-4000	>20ML	*Histioteuthis reversa*	t/st	m	60-1800	186ML
Chiroteuthis joubini	t/st	g	n/a	155ML	*Histioteuthis atlantica*	st/sa	m	0-2500	258ML
Chiroteuthis veryani	st/sa	g	250-2000	91ML	*Histioteuthis* B4	st	m	n/a	n/a
Chiroteuthis sp.	n/a	g	200	107ML	*Histioteuthis* sp. Type B(1)	n/a	n/a	n/a	n/a
Chtenopteryx sp.?	t/st	m	0-2000	83ML	*Histioteuthis* sp. Type B(2)	n/a	n/a	n/a	n/a
Cranchia scabra	t/st	g	190-3500	130ML	*Lepidoteuthis grimaldi*	t/st	m	0-700	970ML
Galiteuthis glacialis	a	m	0-1000	496ML	*Idioteuthis cordiformis*	t/st	m	n/a	87ML
Galiteuthis pacifica	t	m	500-800	65GL	*Mastigoteuthis psychrophile*	a	m	400-1200	n/a
Megalochranchia sp.	t/st	g	0-400	880ML	*Mastigoteuthis* sp.	m	n/a	n/a	n/a
Mesonychoteuthis hamiltoni	sa/a	g	0-2560	4000TL	*Octopoteuthis rugosa*	st	m	?-1500	230ML
Taonius pavo	t/st/sa	g	0-1000	539ML	*Taningia danae*	t/st	m	0-900	>1400ML
Teuthowenia pellucida	st	m	0-2400	200ML	*Nototodarus gouldi*	st	m	100-1130	412ML
Cycloteuthis akimushkini	t/st	m	0-650	480ML	*Ommastrephes bartrami*	st	m	0-2000	800ML

Table 6.6 continued.

Species	Ecotype	Tissue composition	Depth distribution (m)	Maximum GL/ML/TL (mm)
Discoteuthis discus	t/st	m	0-950	155ML
Gonatus antarcticus	a	m	0-2100	345ML
Histioteuthis A1	n/a	n/a	n/a	n/a
Histioteuthis macrohista	st/sa	m	200-2500	67ML
Histioteuthis melaegroteuthis	t/st	m	100-1875	114ML
Histioteuthis bonnelli	st	m	70-2000	330ML
Histioteuthis celetaria pacifica	t	m	200-1200	234ML
Histioteuthis miranda	st	m	0-3000	300ML
Histioteuthis hoylei	t/st	m	100-800	210ML
Histioteuthis sp. Type A (1)	n/a	n/a	n/a	n/a
Todarodes fillapovae	st/sa	m	35-2000	530ML
Kondakovia longimana	a	m	0-860	940ML
Moroteuthis 'A'ingens	sa	m	25-1025	>520ML
Moroteuthis knipovitchi	a	m	0-550	450ML
Moroteuthis lonnbergii	t/st	m	100-920	275ML
Moroteuthis robsoni	st	m	40-260	900ML
Pholidoteuthis adami	t/st	m	360-925	31ML
Pholidoteuthis boschmai	st/sa	m	0-2000	580ML
Vampyroteuthis infernalis	t/st	g	500-4850	100ML

Ecotypes: t: tropical; st: subtropical; sa: sub-Antarctic; a: Antarctic.
Tissue composition: m: muscular; g: gelatinous.
Length: GL: gladius length; ML: maximum dorsal length recorded in mm; TL: maximum total length recorded in mm.
n/a: not available.
Details of cephalopods derived from: Clarke 1966; 1980; 1986; Voss 1969; 1985; McSweeny 1970; 1976; Nesis 1972; 1987; Roper and Young 1975; Imber 1978; Korzun *et al.* 1979; Roper *et al.* 1984; Dunning 1985; 1988; 1993; 1998; Dunning and Brandt 1985; Hatanaka *et al.* 1985; Nemoto *et al.* 1985; Rodhouse and Clarke 1985; Robison 1989; Rodhouse *et al.* 1992; Lipinski 1993; Alexeyev 1994; Lu and Williams 1994; Piatowski and Hagen 1994; Rodhouse and Piatowski 1995; Lordan *et al.* 1998; Rodhouse and Lu 1998; Jackson *et al.* 2000; CIAC Beak Database, Version 1.0, 2001; Collins *et al.* 2001; The Tree of Life Web Project (2001); Cephbase 2002.

6.4. DISCUSSION

The results from this study suggest that southern Australian sperm whales are predominantly teuthophagus, feeding largely on oceanic cephalopods. The diet of these sperm whales demonstrates a high degree of individual variability, suggesting individuals opportunistically consume those species present and most abundant at the time.

Samples attained from stranded animals are subject to a number of biases such as differential digestion of prey items, retention of hard part remains, lack of representation of temporal variability in prey items and inability to discern primary from secondarily digested prey. As a result, the importance of particular prey items may not reflect that of the true diet of the individual. However, obtaining an unbiased assessment of the diet of this species is difficult. Novel techniques such as the analysis of fecal DNA (Jarman *et al.* 2002) in association with investigations into hard part remains may provide a more comprehensive insight into the diet of top predators. Fatty acid signature analysis on blubber derived from live animals via the use of biopsies may provide greater insight into temporal variation in the diet of sperm whales. However, in the Australian region the occurrence and distribution of sperm whales has not yet been established to estimate the viability of fecal sampling or biopsy programs. Fatty acid signature analysis is also limited to coarse scale diet structure and is yet to be proven to be successful at discriminating fine scale diet composition (Bradshaw *et al.* 2003). As a result, stranding events provide a unique window of opportunity into a component of the foraging ecology of sperm whales.

6.4.1. Non-cephalopod component of the diet

Digestion of the soft parts of cephalopods is rapid in sperm whales (Clarke 1980) and that of muscular cephalopod species is more rapid than digestion of teleosts (A. J. Read pers. comm.). Therefore, the lack of fish remains and the presence of cephalopod gladii, eyes, sucker rings and hooks in the stomachs of these animals suggests that fish did not play an important role in the diet of the sperm whales involved in these strandings in the few days prior to the stranding events. In a number of sperm whale diet studies, fish have been observed to be regular but minor contributors to the overall diet of this species (Clarke 1980; Kawakami 1980; Santos *et al.* 1999; see Roe 1969; Martin and Clarke 1986 for exceptions to this). Fish remains were found in 50 % of males in this study in comparison to only 10 % of females and may be indicative of differences in foraging habitats between sexes as suggested in other studies (Clarke *et al.* 1988). However, the number of males in this study was small and may not be representative of the larger

population. Fatty acid signature analysis is in its ability to discriminate coarse scale diet structure (Bradshaw *et al.* 2003) may provide a useful tool to ascertain the importance of fish as an overall group in the diet of sperm whales and any variability in their contribution to the diet both temporally and spatially.

Crustaceans have also been reported in the diet of sperm whales throughout the Southern Hemisphere and include mysids and crabs (Clarke 1980; Clarke *et al.* 1988; Rice 1989). It is not clear whether these are (i) ingested incidentally during normal feeding, (ii) are targeted as specific prey or (iii) are secondarily ingested via the stomachs of fish or squid prey.

Intestinal nematodes are commonly found in large numbers in the stomachs of sperm whales (Rice 1989). If it is assumed that the wet weight of nematodes and the estimated total wet weight of cephalopods in each sample is largely representative of the total wet weight of each stomach sample, nematodes in the stomach of the sperm whales in this study comprise 0.3±0.9 % (range: 0.01-5.7 %) of the total wet weight of stomach contents and so therefore are a relatively minor component of the stomach contents of the sperm whales in this study.

6.4.2. Cephalopod component of the diet

6.4.2.1. Cephalopod species composition

The number of cephalopod species observed in the stomachs of sperm whales in this study is higher than that recorded elsewhere in the Southern Hemisphere (Gaskin and Cawthorn 1967; Clarke and MacLeod 1976a; Clarke and MacLeod 1974; Clarke *et al.* 1976; Clarke 1980; Clarke and MacLeod 1982; Fiscus *et al.* 1989; Pascoe *et al.* 1990; González *et al.* 1994; Smith 1992; Clarke and Roeleveld 1998; Clarke and Roper 1998; Clarke and Young 1998; Smith and Whitehead 2000) and encompasses tropical to Antarctic, muscular and gelatinous, pelagic, mesopelagic, bathypelagic and mesobathypelagic species. The lower species diversity documented in other studies throughout the Southern Hemisphere may be reflective of differences in sampling methodology. Other dietary studies are often composed of very small sample sizes or involve much smaller subsampling proportions than those in this study. These sampling regimes may exclude cephalopod species present in very small numbers in diet samples and therefore, underestimate prey species diversity.

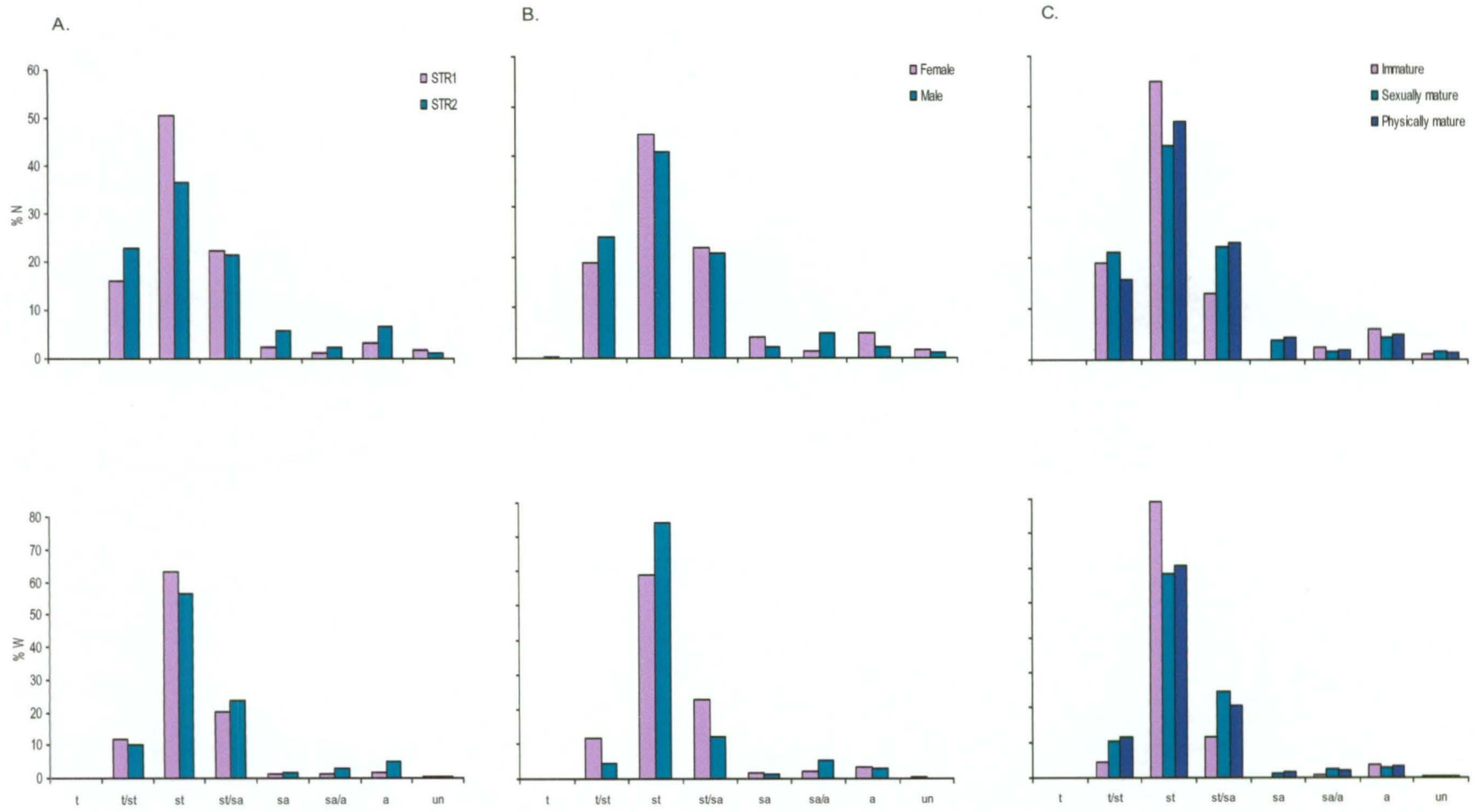


Figure 6.2: Percentage abundance by number (%N) and by estimated wet weight (%W) of cephalopod species ecotype groups for (a) stranding (b) sex and (c) age groups.
Ecotype groups: t: tropical; st: subtropical; sa: subantarctic; a: anatarctic; u: unknown.

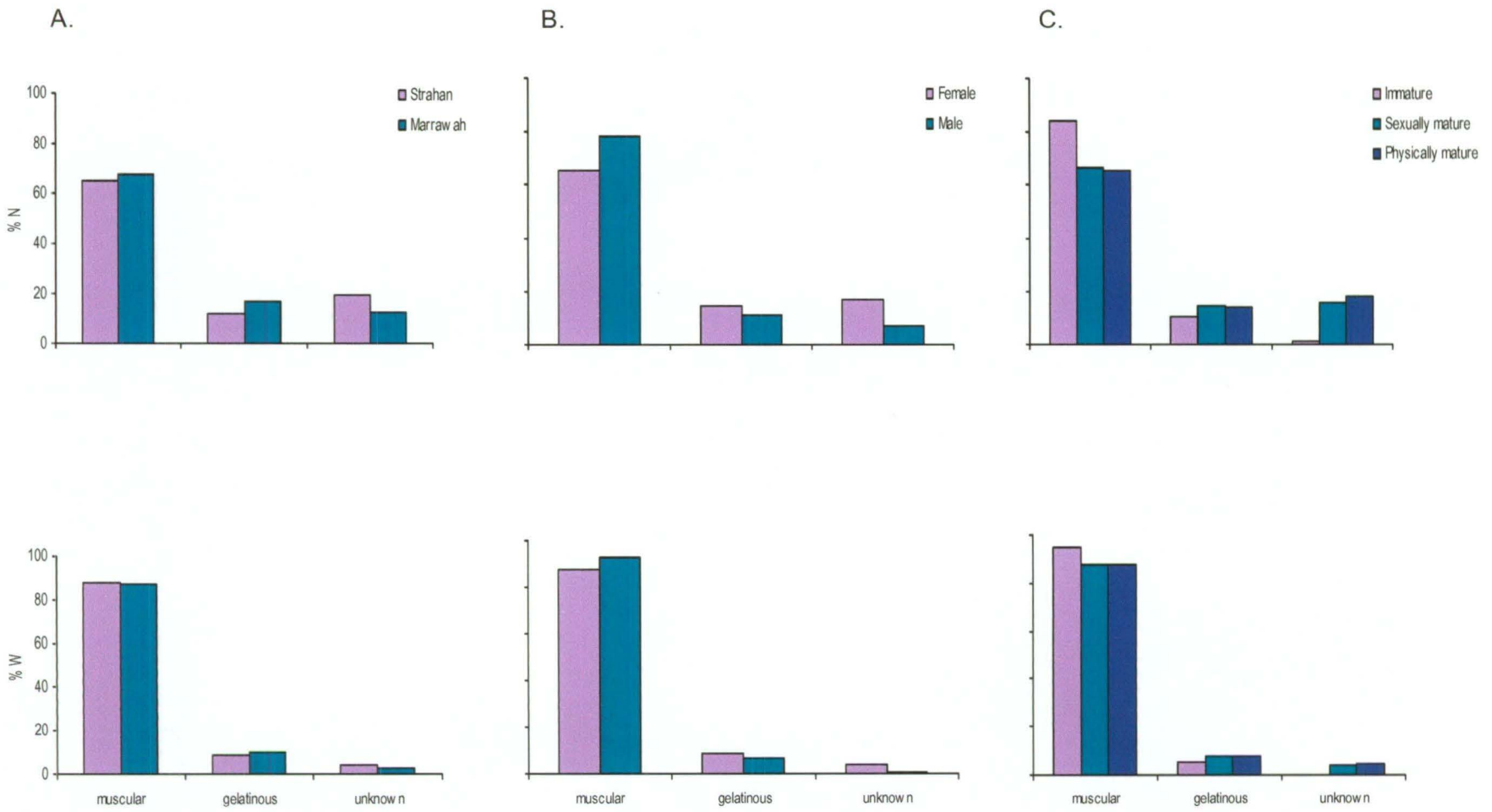


Figure 6.3: Percentage abundance by number (%N) and by estimated wet weight (%W) of muscular and gelatinous cephalopod species for (a) stranding (b) sex and (c) age groups.

Cephalopod species composition in this study was dominated by members of the same families reported in sperm whales from other areas of the Southern Hemisphere: the Histioteuthidae, Onychoteuthidae, Ommastrephidae, Cranchiidae and Pholidoteuthidae families (Pascoe *et al.* 1990; Clarke *et al.* 1976; Clarke *et al.* 1988; Clarke *et al.* 1980; Clarke and Roeleveld 1998; Clarke 1980; Clarke and MacLeod 1982; Clarke and Roper 1998; Gaskin and Cawthorn 1967; Mikhalev *et al.* 1981). The Histioteuthidae appear to be an important family numerically in the diet of sperm whales in temperate waters globally (Clarke 1980; Kawakami 1980; Clarke 1996; Clarke and Young 1998).

6.4.2.2. Size of cephalopods

The maximum calculated mantle lengths in this study were often larger than that reported for cephalopod species in the literature. Cephalopods are difficult to sample using conventional methods. Large individuals often avoid nets and are therefore under-represented in samples (Clarke 1983). It is possible that cephalopod predators are more efficient at catching these size classes and therefore, provide a more accurate assessment of cephalopod size structure (Clarke 1983). Lower rostral lengths of cephalopods ranged over similar sizes or encompassed that found in the diet of sperm whales in other regions (Clarke and Macleod 1974; Clarke and Macleod 1976; Clarke 1980; Fiscus *et al.* 1989; Smith 1992; Clarke and Young 1998; Smith and Whitehead 2000).

While cephalopods less than 300 mm DML dominated the diet, larger species actually contributed a far greater proportion to the biomass of the stomach contents of these animals, with those larger than 1,000 gm in estimated wet weight comprising 78.6 % of the total estimated wet mass. The irregular consumption of larger species appears to be an important, efficient source of energy for an animal that is estimated to consume between 3-4 % of its own body mass per day (Lockyer 1981b). If the average weight of prey consumed is 233.7 gm and the average weight of the sperm whales in this study is 12.3 tons ($W_t=0.006648L_m^{3.18}$, Lockyer 1981b), the estimated number of prey items eaten by an individual (calculated as the mean of 3-4 %) would equate to 1,842.1 individuals per day. This clearly highlights the importance of larger species as an efficient means of acquiring energy, thereby reducing the number of prey items required to meet energetic demands.

Table 6.7: Mean lower rostral lengths±SD (n) in mm of cephalopod species in the stomachs of sperm whales from Tasmania.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)	Range
Haliphron atlanticus	14.6±3.7 (12)	11.5±2.8 (3)	15.6±3.5 (9)	—	14.5±4.0 (10)	—	14.9±3.9 (10)	—	14.8±4.3 (8)	—	13.0±2.5 (2)	—	13.0±2.5 (2)	9.6-22.4
Ancistrocheirus lesueuri	7.3±1.2 (1043)	7.4±1.2 (501)	7.3±1.2 (542)	7.6±0.6 (3)	7.3±1.1 (353)	7.3±1.2 (447)	7.4±1.2 (1029)	—	7.3±1.1 (342)	7.3±1.2 (447)	7.2±1.0 (14)	7.8±0.7 (2)	7.1±1.1 (12)	3.8-14.4
Architeuthis sp.	12.0±2.7 (215)	12.1±2.5 (191)	11.2±4.1 (24)	—	11.4±2.9 (61)	12.2±2.8 (110)	12.0±2.7 (214)	—	11.3±2.8 (60)	12.0±2.7 (102)	17.3 (1)	—	17.3 (1)	4.7-18.7
Japetella sp.	4.7±2.1 (39)	3.7±1.3 (8)	4.9±2.2 (31)	—	6.3±2.2 (17)	3.3±0.6 (6)	4.7±2.1 (38)	—	6.4±2.2 (16)	3.3±0.6 (6)	4.4 (1)	—	4.4 (1)	2.5-8.7
Chiroteuthis joubini	7.4±0.7 (316)	7.4±0.9 (221)	7.4±0.8 (95)	4.9 (1)	7.3±0.8 (56)	7.4±0.9 (184)	7.4±0.8 (314)	4.9 (1)	7.3±0.6 (58)	7.3±0.7 (147)	9.7±1.3 (2)	—	9.7±1.3 (2)	3.9-12.8
Chiroteuthis veryani	6.7±0.7 (1361)	6.7±0.7 (697)	6.8±0.8 (664)	5.9 (1)	6.7±0.7 (489)	6.7±0.7 (678)	6.7±0.7 (1327)	—	6.7±0.7 (456)	6.7±0.7 (617)	6.9±0.8 (34)	5.9 (1)	7.0±0.7 (33)	3.4-8.6
Chiroteuthis sp.	7.9±1.7 (15)	8.2±0.4 (3)	7.8±1.9 (12)	5.9 (1)	8.3±1.6 (11)	7.2±1.9 (3)	8.0±1.7 (14)	—	8.3±1.6 (11)	6.9±2.6 (2)	5.9 (1)	5.9 (1)	—	5.0-9.7
Chtenopteryx sp.?	1.5 (1)	1.5 (1)	—	—	—	1.5 (1)	1.5 (1)	—	—	1.5 (1)	—	—	—	1.5
Cranchia scabra	3.4±0.5 (60)	3.3±0.5 (15)	3.5±0.5 (45)	—	3.3±0.5 (23)	3.6±0.4 (19)	3.4±0.5 (60)	—	3.3±0.5 (23)	3.6±0.4 (19)	—	—	—	2.1-4.6
Galiteuthis glacialis	5.7±0.8 (1279)	5.8±0.9 (411)	5.7±0.7 (868)	4.7±0.6 (4)	5.5±0.8 (525)	5.7±0.8 (543)	5.7±0.8 (1263)	4.0 (1)	5.5±0.8 (510)	5.7±0.8 (545)	5.7±0.8 (16)	5.0±0.5 (3)	5.8±0.8 (13)	1.3-8.4
Galiteuthis pacifica	4.8±0.9 (5)	4.8±1.0 (4)	4.8 (1)	—	5.4±0.6 (3)	4.0±0.4 (2)	4.8±0.9 (5)	—	5.4±0.6 (3)	4.0±0.4 (3)	—	—	—	3.7-5.9
Megalochranchia sp.	8.4±1.8 (214)	8.0±1.5 (56)	8.5±1.8 (158)	—	8.3±1.9 (73)	8.4±1.8 (102)	8.4±1.8 (214)	—	8.4±1.9 (73)	8.3±1.8 (103)	—	—	—	4.3-12.8
Mesonychoteuthis hamiltoni	14.6±5.8 (770)	14.1±4.9 (264)	14.8±6.2 (506)	16.5±3.2 (2)	15.2±6.3 (309)	14.3±5.6 (351)	14.0±5.4 (672)	—	13.7±5.2 (213)	14.3±5.6 (351)	18.3±7.3 (98)	16.5±3.2 (2)	18.3±7.3 (96)	2.9-40.7
Taonius pavo	8.8±1.0 (932)	8.7±1.0 (709)	9.0±0.9 (223)	9.5 (1)	8.7±1.0 (310)	8.7±1.0 (481)	8.8±1.0 (915)	—	8.7±1.0 (294)	8.7±1.0 (481)	9.2±0.9 (17)	9.5 (1)	9.2±0.9 (16)	5.4-12.9

Table 6.7 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)	Range
Teuthowenia pellucida	7.4±0.8 (822)	7.3±0.8 (439)	7.5±0.7 (383)	8.3±0.6 (2)	7.3±0.8 (266)	7.4±0.8 (391)	7.4±0.8 (81)	—	7.3±0.8 (255)	7.4±0.8 (392)	7.7±0.6 (12)	8.3±0.6 (2)	7.5±0.5 (10)	3.4-9.6
Cycloteuthis akimushkini	7.5±1.8 (4)	4.8 (1)	8.4±0.2 (3)	—	8.4±0.2 (3)	—	7.5±1.8 (4)	—	8.4±0.2 (3)	—	—	—	—	4.8-8.5
Discoteuthis discus	7.2±0.8 (14)	7.2±0.8 (13)	6.8 (1)	—	7.3±0.8 (6)	7.1 (1)	7.2±0.8 (13)	—	7.4±0.8 (5)	7.1 (1)	6.8 (1)		6.8 (1)	5.5-8.4
Gonatus antarcticus	6.8±0.6 (59)	6.8±0.6 (46)	6.9±0.5 (13)	—	6.8±0.6 (24)	7.0±0.5 (27)	6.8±0.6 (58)	—	6.7±0.6 (23)	7.0±0.5 (27)	7.8 (1)	7.8 (1)	—	5.2-8.2
Histioteuthis A1	5.7±0.6 (65)	5.7±0.6 (65)	—	—	—	5.7±0.6 (59)	5.7±0.6 (65)	—	—	5.7±0.6 (65)	—	—	—	3.8-7.4
Histioteuthis macrohista	4.7±1.2 (275)	3.3±0.3 (64)	5.2±1.1 (211)	3.5 (1)	4.4±1.3 (69)	5.0±1.1 (190)	4.8±1.2 (274)	3.5 (1)	4.4±1.3 (68)	5.0±1.1 (190)	2.8 (1)	—	2.8 (1)	2.4-7.4
Histioteuthis melaegroteuthis	3.1±0.3 (317)	3.1±0.2 (103)	3.2±0.3 (214)	—	3.1±0.2 (117)	3.2±0.3 (127)	3.2±0.3 (310)	—	3.1±0.2 (110)	3.2±0.3 (128)	3.1±0.2 (7)	—	3.1±0.2 (7)	2.3-4.8
Histioteuthis bonnelli	5.7±0.6 (2524)	5.7±0.6 (947)	5.7±0.6 (1577)	5.3±0.5 (9)	5.7±0.6 (885)	5.6±0.6 (1194)	5.7±0.6 (2501)	—	5.7±0.6 (871)	5.6±0.6 (1194)	5.5±0.5 (23)	5.3±0.5 (9)	5.7±0.5 (14)	2.7-7.9
Histioteuthis celetaria pacifica	6.3±1.1 (16)	6.0±1.2 (8)	6.7±1.1 (8)	—	7.0±1.4 (4)	6.4±0.5 (9)	6.1±1.0 (12)	—		6.4±0.5 (9)	7.0±1.4 (4)	—	7.0±1.4 (4)	3.3-8.9
Histioteuthis miranda	6.5±0.6 (510)	6.5±0.6 (183)	6.5±0.6 (327)	6.1±0.0 (2)	6.4±0.6 (192)	6.4±0.5 (207)	6.5±0.6 (501)	—	6.4±0.6 (184)	6.4±0.5 (208)	6.5±0.9 (9)	6.1±0.0 (2)	6.6±1.1 (7)	4.3-8.7
Histioteuthis hoylei	6.1±0.8 (969)	6.2±0.8 (419)	6.1±0.8 (550)	6.3±0.2 (2)	6.1±0.8 (437)	6.0±0.8 (338)	6.1±0.8 (941)	—	6.1±0.8 (411)	6.0±0.8 (338)	6.1±0.8 (28)	6.3±0.2 (2)	6.1±0.8 (26)	3.6-9.2
Histioteuthis sp. Type A (1)	6.1±0.9 (158)	6.1±0.9 (139)	6.3±1.1 (19)	—	6.2±1.0 (56)	5.9±0.7 (83)	6.1±0.9 (158)	—	6.2±1.0 (56)	5.9±0.7 (83)	—	—	—	3.8-7.4
Histioteuthis B1	5.6±0.7 (1259)	5.6±0.6 (1149)	5.6±1.0 (114)	—	5.4±0.8 (159)	5.7±0.6 (837)	5.6±0.7 (1249)	—	5.3±0.8 (145)	5.7±0.6 (837)	6.0±0.4 (14)	—	6.0±0.4 (14)	3.0-7.5
Histioteuthis eltaninae	4.7±0.3 (1810)	4.7±0.3 (566)	4.7±0.3 (1240)	—	4.7±0.3 (562)	4.7±0.3 (965)	4.7±0.3 (1781)	—	4.7±0.3 (541)	4.7±0.3 (965)	4.8±0.2 (25)	—	4.8±0.2 (25)	2.6-6.3
Histioteuthis B2	5.2±0.7 (6186)	5.3±0.7 (3755)	5.0±0.6 (2431)	5.3 (1)	5.2±0.7 (2150)	5.2±0.7 (3246)	5.2±0.7 (6088)	—	5.2±0.7 (2053)	5.2±0.7 (3246)	5.3±0.6 (98)	5.3 (1)	5.3±0.6 (97)	2.5-8.0

Table 6.7 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)	Range
Histioteuthis reversa	4.8±0.5 (345)	4.9±0.4 (123)	4.8±0.5 (222)	4.8±0.3 (5)	4.8±0.5 (251)	4.8±0.5 (81)	4.8±0.5 (316)	—	4.9±0.5 (227)	4.8±0.5 (81)	4.7±0.5 (29)	4.8±0.3 (5)	4.7±0.5 (24)	3.5-6.1
Histioteuthis atlantica	5.2±0.6 (4635)	5.3±0.6 (2916)	5.2±0.7 (1719)	5.1±0.9 (3)	5.3±0.6 (1560)	5.2±0.6 (2466)	5.2±0.6 (4435)	—	5.3±0.6 (1363)	5.2±0.6 (2466)	5.3±0.6 (200)	5.1±0.9 (3)	5.3±0.6 (197)	3.1-7.9
Histioteuthis B4	5.4±0.6 (7011)	5.4±0.6 (5333)	5.4±0.7 (1677)	5.1±0.5 (21)	5.4±0.6 (2065)	5.3±0.6 (3714)	5.4±0.6 (6652)	4.8±0.6 (11)	5.4±0.6 (1717)	5.3±0.6 (3718)	5.4±0.6 (358)	5.3±0.3 (10)	5.4±0.6 (348)	2.5-7.8
Histioteuthis sp. Type B(1)	5.9±0.8 (168)	5.9±0.8 (113)	5.9±0.7 (55)	—	6.2±0.6 (57)	5.9±0.7 (50)	5.9±0.8 (168)	—	6.2±0.6 (57)	5.9±0.7 (50)	—	—	—	3.5-7.2
Histioteuthis sp. Type B(2)	5.5±0.7 (281)	5.6±0.7 (159)	5.4±0.7 (122)	—	5.7±0.7 (112)	5.4±0.6 (115)	5.5±0.7 (261)	—	5.7±0.7 (92)	5.4±0.6 (115)	5.5±0.5 (20)	—	5.5±0.5 (20)	3.8-7.1
Lepidoteuthis grimaldi	11.7±2.6 (2251)	12.3±2.6 (1143)	11.1±2.4 (1108)	—	11.3±2.3 (915)	11.9±2.4 (1012)	11.7±2.6 (2139)	—	11.3±2.3 (803)	11.8±2.4 (1012)	11.5±2.6 (112)	—	11.5±2.6 (112)	6.2-23.5
Idioteuthis cordiformis	6.5±1.0 (442)	6.2±0.8 (171)	6.6±1.1 (271)	7.1 (1)	6.6±1.0 (169)	6.5±0.9 (173)	6.5±1.0 (418)	—	6.6±1.0 (146)	6.5±0.9 (173)	6.5±1.0 (24)	7.1 (1)	6.5±1.0 (23)	4.0-11.6
Mastigoteuthis psychrophile	4.2±0.6 (3)	3.9±0.2 (2)	4.8 (1)	—	4.2±0.6 (3)		4.2±0.6 (3)	—	4.2±0.6 (3)	—	—	—	—	3.7-2.8
Mastigoteuthis sp.	4.7±0.8 (25)	4.5±0.7 (9)	4.8±0.8 (16)	—	5.2±0.2 (4)	4.6±0.9 (18)	4.7±0.8 (24)	—	5.2±0.3 (3)	4.6±0.9 (18)	5.1 (1)	—	5.1 (1)	3.3-6.5
Octopoteuthis rugosa	10.9±2.2 (709)	11.4±2.3 (403)	10.2±1.8 (306)	—	10.7±2.1 (260)	10.8±1.9 (328)	10.9±2.2 (673)	—	10.7±2.0 (224)	10.8±1.9 (328)	11.0±2.3 (36)	—	11.0±2.3 (36)	6.6-20.5
Taningia danae	15.6±3.5 (278)	15.4±3.6 (215)	16.5±3.0 (63)	—	15.7±3.4 (88)	15.4±3.7 (158)	15.6±3.6 (268)	—	15.6±3.5 (78)	15.4±3.7 (158)	17.0±2.2 (10)	—	17.0±2.2 (10)	8.8-23.2
Nototodarus gouldi	12.1±1.5 (305)	12.4±1.2 (190)	11.5±1.6 (115)	9.8 (1)	11.9±1.6 (92)	12.0±1.5 (125)	12.1±1.5 (281)	—	11.8±1.7 (69)	12.0±1.5 (125)	12.1±1.2 (24)	9.8 (1)	12.2±1.1 (23)	5.2-14.8
Ommastrephes bartrami	12.8±1.4 (49)	12.6±1.4 (33)	13.1±1.4 (16)	—	13.0±1.9 (17)	12.7±1.2 (18)	12.8±1.4 (49)	—	13.0±1.9 (17)	12.7±1.2 (18)	—	—	—	7.2-15.2
Todarodes fillapovae	11.9±1.4 (1085)	12.1±1.4 (634)	11.7±1.3 (451)	12.7±1.4 (4)	11.9±1.4 (413)	12.0±1.3 (424)	11.9±1.4 (1063)	12.0±1.5 (2)	11.9±1.4 (393)	12.0±1.3 (424)	12.3±2.0 (22)	13.5±1.3 (2)	12.1±2.0 (20)	4.3-15.8
Kondakovia longimana	10.9±2.8 (518)	10.0±2.3 (196)	11.4±2.9 (322)	8.7±2.5 (6)	11.3±3.1 (135)	11.0±2.6 (222)	10.8±2.7 (494)	—	11.1±3.1 (117)	11.0±2.6 (222)	11.6±3.3 (24)	8.7±2.5 (6)	12.6±3.0 (18)	5.3-21.2

Table 6.7 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)	Range
Moroteuthis 'A'/ingens	10.5±1.2 (113)	10.2±1.3 (73)	10.9±0.8 (40)	—	10.2±1.2 (41)	10.6±1.3 (52)	10.5±1.3 (99)	—	10.0±1.3 (27)	10.6±1.3 (52)	10.5±0.8 (14)	—	10.6±0.9 (14)	3.2-12.2
Moroteuthis knipovitchi	4.9±0.6 (314)	4.9±0.7 (153)	4.9±0.4 (161)	—	4.8±0.5 (65)	4.9±0.6 (196)	4.9±0.6 (312)	—	4.8±0.5 (63)	4.9±0.6 (196)	5.0±0.5 (2)	—	5.0±0.5 (2)	3.0-8.0
Moroteuthis lonnbergii	6.3±0.7 (204)	6.6±0.6 (90)	6.0±0.6 (114)	—	6.0±0.6 (84)	6.4±0.6 (74)	6.3±0.7 (190)	—	6.1±0.7 (70)	6.4±0.6 (74)	5.9±0.5 (14)	—	5.9±0.5 (14)	3.4-7.7
Moroteuthis robsoni	9.2±1.2 (1288)	9.0±1.4 (486)	9.3±1.1 (802)	9.2±0.9 (9)	9.1±1.3 (587)	9.4±1.1 (482)	9.1±1.3 (1113)	—	8.9±1.4 (421)	9.4±1.1 (482)	9.6±0.8 (177)	9.2±0.9 (9)	9.4±0.9 (166)	4.5-12.3
Pholidoteuthis adami	4.6±1.1 (14)	4.6±1.4 (9)	4.4±0.6 (5)	—	4.4±0.9 (12)	5.7±2.2 (2)	4.6±1.1 (14)	—	4.4±0.9 (12)	5.7±2.2 (2)	—	—	—	2.8-7.2
Pholidoteuthis boschmai	9.8±1.7 (2131)	9.7±2.0 (809)	9.8±1.5 (1322)	—	9.9±1.6 (942)	9.7±1.7 (848)	9.8±1.7 (2027)	—	9.8±1.6 (838)	9.7±1.7 (899)	10.3±1.1 (104)	—	10.3±1.1 (104)	5.4-18.1
Vampyroteuthis infernalis	10.7±2.1 (20)	10.1±2.0 (16)	12.7±1.3 (4)	—	10.4±2.6 (9)	10.7±1.8 (9)	10.4±2.0 (19)	—	9.9±2.3 (8)	10.7±1.8 (9)	14.5 (1)	—	14.5 (1)	5.5-14.5

6.4.2.3. Cephalopod species composition and size with respect to stranding group, sex and age

Although significant differences were found in the species composition of the diet of individuals on the basis of stranding site and sex and in the size of prey items on the basis of stranding site and age, high individual variability was observed within all groups.

The social structure of female sperm whale groups is such that each group is based on a dynamic association of smaller units comprised of long-term relationships between 12 to 13 individuals that may or may not be related to each other (Whitehead *et al.* 1991; Whitehead and Kahn 1992; Mesnick *et al.* 2003). Preliminary genetic analyses support the presence of smaller units comprised of related and unrelated individuals in the stranding groups studied here (Mesnick *et al.* 2001, 2003). It is therefore probable that the two stranding groups (STR1: n=66; STR2: n=35) are composed of several of these dynamic associations and that therefore, differences between stranding sites are more reflective of differences in the diet of individuals in these smaller units. Moreover, sperm whales observed in the field while associating with others in their group at the surface, separate three-dimensionally on diving (Watkins and Schevill 1977). Separation of foraging individuals is advantageous as it prevents animals from searching through low prey density areas recently encountered by other whales. Separation of foraging individuals would be expected to result in at least some degree of individual variation in prey items encountered and therefore, overall diet.

Differences in the species composition of the diet of males and females may be reflective of different foraging habitats between sexes. The ages of males ranged between five and 24 years, the majority of which (five of six) were between 19 and 24 years and involved in STR2. It is not clear at what age males disperse from their natal groups. Dispersal is reported to occur at six to ten years (Best 1979; Richard *et al.* 1996) or 15 years (Rice 1989). However, on leaving their natal groups males associate with others of a similar size rather than age group, with groups observed to contain 12 to 15 individuals (or multiples thereof) ten to 29 years in age (Best 1979). It is possible that the males in this study (excluding the five year old which is likely to have been associated with its maternal unit) were part of a bachelor group of males foraging in a similar area, but separate to the female groups in this study and had joined the female groups just prior to the strandings.

Table 6.8: Calculated mean mantle lengths±SD (n) in mm of cephalopod species in the stomach contents of sperm whales from Tasmania (n, range)

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Haliphron atlanticus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Ancistrocheirus lesueuri	259.3±48.0 (113.6-544.9; 1043)	261.3±48.4 (501)	257.4±47.6 (542)	269.8±23.5 (3)	255.0±46.6 (353)	257.3±47.7 (447)	259.4±48.1 (1029)	—	255.2±46.6 (342)	257.3±47.7 (102)	253.3±42.4 (14)	276.6±28.8 (2)	249.4±43.9 (12)
Architeuthis sp.	655.7±164.0 (223.2-1053.5; 215)	662.0±151.1 (191)	605.7±242.2 (24)	—	628.6±178.9 (61)	649.8±158.0 (101)	654.2±162.9 (214)	—	615.8±167.0 (60)	653.8±162.2 (102)	970.5 (1)	—	970.5 (1)
Japetella sp.	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Chiroteuthis joubini	192.2±20.7 (106.8-324.5; 316)	192.0±20.9 (221)	192.9±20.4 (95)	131.3 (1)	191.3±17.9 (60)	189.8±17.9 (147)	191.9±20.3 (314)	131.3 (1)	189.3±14.1 (58)	189.8±17.9 (147)	247.4±32.9 (2)	—	247.4±32.9 (2)
Chiroteuthis veryani	175.3±17.9 (94.6-221.8; 1361)	174.0±17.0 (697)	176.6±18.7 (664)	199.1 (1)	175.3±17.9 (487)	175.8±17.4 (617)	175.1±17.8 (1327)	—	175.0±17.9 (456)	175.8±17.4 (617)	182.2±18.1 (34)	199.1 (1)	181.7±18.2 (33)
Chiroteuthis sp.	207.4±39.6 (133.7-248.7; 15)	212.0±10.7 (3)	206.2±44.4 (12)	199.1 (1)	213.5±39.7 (11)	187.5±47.6 (3)	208.0±41.1 (14)	—	213.5±39.7 (11)	187.5±47.6 (3)	199.1 (1)	199.1 (1)	—
Chtenopteryx sp.?	60.3 (1)	60.3 (1)	—	—	—	60.3 (1)	60.3 (1)	—	—	60.3 (1)	—	—	—
Cranchia scabra	148.4±26.5 (76.6-198.1; 60)	151.4±18.8 (15)	147.4±28.8 (45)	—	151.2±17.5 (23)	164.1±14.5 (19)	113.7±13.9 (60)	—	23.0±17.5 (23)	164.1±14.5 (19)	—	—	—
Galiteuthis glacialis^	483.8±68.3 (115.7-710.5; 1279)	490.6±72.4 (411)	480.6±66.1 (868)	402.6±52.7 (4)	468.6±69.7 (523)	485.5±63.4 (545)	484.8±65.7 (1263)	341.8 (1)	470.5±63.8 (510)	485.5±63.4 (545)	399.5±162.4 (16)	422.8±41.3 (3)	394.1±180.3 (13)
Galiteuthis pacifica	408.8±74.2 (316.7-501.0; 5)	408.8±85.7 (4)	408.8 (1)	—	456.3±46.1 (3)	337.6±29.6 (2)	408.8±74.2 (5)	—	456.3±46.1 (3)	337.6±29.6 (2)	—	—	—
Megalochranchia sp.	518.0±125.9 (222.1-902.9; 214)	552.4±121.3 (56)	505.8±125.7 (158)	—	555.6±134.7 (73)	497.8±132.8 (103)	518.0±125.9 (214)	—	555.6±134.7 (73)	497.8±132.8 (103)	—	—	—
Mesonychoteuthis hamiltoni	886.6±359.7 (165.9-2640.7; 770)	911.6±362.5 (408)	896.5±382.4 (506)	939.6±195.5 (2)	919.2±386.6 (309)	874.2±352.2 (351)	854.1±333.5 (672)	—	831.8±319.2 (213)	874.2±352.2 (351)	1109.5±446.1 (98)	939.6±195.5 (2)	1113.1±449.7 (96)

Table 6.8 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Taonius pavo	527.1±61.8 (319.4-780.2; 932)	522.8±63.0 (709)	540.9±55.8 (223)	571.3 (1)	523.4±59.9 (310)	523.0±62.7 (481)	526.6±61.8 (915)	—	294±521.8 (294)	522.9±62.6 (481)	553.6±55.9 (17)	571.3 (1)	552.5±57.5 (16)
Teuthowenia pellucida	244.2±23.8 (123.9-367.0; 822)	241.8±25.3 (439)	246.9±21.7 (383)	350.7±23.1 (2)	239.9±25.0 (265)	244.5±23.5 (392)	243.9±23.3 (810)	—	239.6±25.3 (255)	244.5±23.5 (392)	264.3±43.3 (12)	350.7±23.1 (2)	247.1±15.6 (10)
Cycloteuthis akimushkini	231.7±55.6 (148.8-263.5; 4)	148.8 (1)	259.4±7.2 (3)	—	259.4±7.2 (3)	—	231.7±55.6 (4)	—	259.4±7.2 (3)	—	—	—	—
Discoteuthis discus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Gonatus antarcticus	250.2±26.2 (179.5-308.1; 59)	249.0±27.5 (46)	254.1±21.9 (13)	—	247.2±26.6 (24)	255.9±22.3 (27)	249.4±25.9 (58)	—	245.3±25.5 (23)	255.9±22.3 (27)	291.0 (1)	—	291.0 (1)
Histioteuthis A1	164.8±21.5 (101.0-221.2; 65)	164.8±21.5 (65)	—	—	—	164.8±20.6 (59)	164.8±21.5 (65)	—	—	164.8±20.6 (59)	—	—	—
Histioteuthis macrohista	70.8±18.2 (35.2-106.5; 275)	49.4±5.3 (64)	77.3±15.5 (211)	53.0 (1)	66.3±19.2 (69)	74.4±16.6 (190)	70.9±18.1 (274)	52.0 (1)	66.6±19.2 (68)	74.4±16.6 (190)	42.9 (1)	—	42.9 (1)
Histioteuthis melaegroteuthis	63.8±12.6 (37.5-94.4; 317)	79.1±6.3 (103)	56.4±7.0 (214)	—	56.1±4.8 (117)	57.6±7.1 (128)	64.0±12.7 (310)	—	66.0±12.9 (110)	62.4±10.7 (128)	54.9±3.7 (7)	—	54.9±3.7 (7)
Histioteuthis bonnelli[#]	88.3±8.9 (43.0-122.2; 2523)	88.8±9.4 (947)	87.9±8.6 (1576)	82.4±7.4 (9)	88.7±9.1 (885)	87.4±9.0 (1193)	88.3±8.9 (2500)	—	88.7±9.1 (871)	87.4±9.0 (1193)	86.3±8.0 (23)	82.4±7.4 (9)	88.8±7.6 (14)
Histioteuthis celetaria pacifica	176.3±35.0 (84.4-221.2; 16)	173.2±38.8 (8)	179.4±33.1 (8)	—	184.4±19.1 (4)	189.3±18.3 (9)	173.6±39.2 (12)	—	—	189.3±18.3 (9)	184.4±19.1 (4)	—	184.4±19.1 (4)
Histioteuthis miranda	195.1±20.0 (120.6-271.1; 510)	195.0±19.3 (183)	195.1±20.4 (327)	182.2±0.0 (2)	192.2±20.6 (191)	193.5±18.2 (208)	195.1±19.7 (501)	—	184.0±192.0 (184)	193.5±18.2 (208)	194.7±32.1 (9)	182.2±0.0 (2)	198.3±36.1 (7)
Histioteuthis hoylei	95.7±12.0 (60.1-141.6; 969)	97.5±11.5 (419)	94.4±12.3 (550)	98.6±3.1 (2)	97.0±11.1 (437)	91.6±12.0 (338)	95.7±12.0 (941)	—	411.0±97.0 (411)	91.6±12.0 (338)	96.5±11.1 (28)	98.6±3.1 (2)	96.4±11.5 (26)
Histioteuthis sp. Type A (1)	187.5±31.0 (84.4-237.9; 93)	188.4±29.9 (74)	183.9±35.6 (19)	—	182.6±32.6 (56)	189.5±25.7 (24)	187.5±31.0 (93)	—	182.6±32.6 (56)	189.5±25.7 (24)	—	—	—

Table 6.8 continued.

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Histioteuthis B1	110.8±15.1 (53.0-153.0; 1259)	110.7±14.1 (1149)	111.8±23.1 (110)	—	106.3±18.5 (159)	112.7±13.4 (837)	110.7±15.1 (1245)	—	105.0±18.7 (145)	112.7±13.4 (837)	119.7±9.0 (14)	—	119.7±9.0 (14)
Histioteuthis eltaninae	90.4±7.0 (48.6-126.3; 1810)	90.3±7.4 (566)	90.4±6.9 (1244)	—	90.2±7.0 (566)	90.5±7.1 (837)	90.4±7.0 (1785)	—	90.1±7.1 (541)	90.5±7.1 (965)	91.9±5.0 (25)	—	91.9±5.0 (25)
Histioteuthis B2	101.9±14.8 (41.9-164.1; 6186)	105.1±14.5 (3755)	96.9±13.9 (2431)	104.1 (1)	102.2±15.1 (2150)	101.9±14.6 (3246)	101.9±14.8 (6088)	—	102.1±15.2 (2053)	101.9±14.6 (3246)	103.1±13.0 (98)	104.1 (1)	103.1±13.1 (97)
Histioteuthis reversa	93.7±10.3 (64.1-121.9; 345)	95.1±9.5 (123)	93.0±10.7 (222)	93.5±7.3 (5)	94.0±10.6 (251)	92.8±10.1 (81)	94.0±10.3 (316)	—	94.4±10.5 (227)	92.8±10.1 (81)	91.3±10.5 (29)	93.5±7.3 (5)	90.9±11.2 (24)
Histioteuthis atlantica[#]	123.8±16.2 (69.1-192.3; 4634)	124.7±15.7 (2916)	122.3±17.0 (1718)	119.6±23.8 (3)	124.6±16.2 (1560)	123.6±16.3 (2466)	123.7±16.3 (4434)	—	124.4±16.3 (1363)	123.6±16.3 (2465)	126.0±15.2 (200)	119.6±23.8 (3)	126.1±15.1 (197)
Histioteuthis B4	105.5±14.0 (41.9-159.6; 7011)	105.6±13.9 (5333)	105.4±14.4 (1678)	104.7±12.2 (21)	106.3±14.1 (2065)	104.8±13.9 (3718)	105.6±14.1 (6653)	94.0±13.8 (11)	106.4±14.2 (1717)	104.8±13.9 (3718)	105.4±13.4 (358)	104.1±7.5 (10)	105.4±13.6 (348)
Histioteuthis sp. Type B(1)	117.2±17.3 (64.1-146.3; 168)	116.5±18.5 (113)	118.5±14.7 (55)	—	123.7±14.2 (57)	117.9±14.5 (50)	117.2±17.3 (168)	—	123.7±14.2 (57)	117.9±14.5 (50)	—	—	—
Histioteuthis sp. Type B(2)	109.2±15.2 (70.8-144.1; 281)	110.5±14.7 (159)	107.5±15.8 (122)	—	112.5±15.0 (112)	106.0±14.0 (115)	109.2±15.5 (261)	—	113.2±15.7 (92)	106.0±14.0 (115)	109.2±10.9 (20)	—	109.2±10.9 (20)
Lepidoteuthis grimaldi	577.7±123.9 (302.9-1172.7; 2144)	606.7±122.4 (1037)	550.4±119.1 (1107)	—	561.6±116.5 (917)	588.3±121.5 (1009)	577.9±123.4 (2032)	—	560.1±114.1 (805)	588.3±121.5 (1009)	573.0±132.5 (112)	—	573.0±132.5 (112)
Idioteuthis cordiformis	186.5±30.5 ((20.6-335.5; 442)	180.0±23.2 (171)	190.6±33.7 (271)	20.6 (1)	189.5±29.7 (169)	187.6±26.4 (173)	186.9±29.5 (418)	—	190.1±29.8 (146)	187.6±26.4 (173)	178.8±44.0 (24)	20.6 (1)	185.7±28.9 (23)
Mastigoteuthis psychrophile	120.3±3.5 (117.4-124.2; 3)	118.3±1.3 (2)	124.2 (1)	—	120.3±3.5 (3)		120.3±3.5 (3)	—	120.3±3.5 (3)	—	—	—	—
Mastigoteuthis sp.	135.3±23.0 (64.2-187.2; 25)	129.7±20.2 (9)	138.7±24.6 (16)	—	149.4±6.3 (4)	132.1±25.9 (18)	134.9±23.4 (24)	—	150.4±7.3 (3)	132.1±25.9 (18)	146.5 (1)	—	146.5 (1)
Octopoteuthis rugosa	187.5±38.2 (23.6-354.9; 709)	196.4±40.6 (403)	175.7±31.3 (306)	—	186.5±36.1 (260)	186.2±34.1 (328)	187.3±38.2 (673)	—	185.8±35.5 (224)	186.2±34.1 (328)	190.3±40.4 (36)	—	190.3±40.4 (36)

Species	All (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Taningia danae	618.4±265.6 (105.0-1188.2; 278)	598.4±273.3 (215)	686.9±226.1 (63)	—	625.8±253.3 (88)	604.8±275.2 (158)	614.6±268.1 (268)	—	613.6±260.9 (78)	604.8±275.2 (158)	720.3±163.6 (10)	—	720.3±163.6 (10)
Nototodarus gouldi	455.3±50.4 (218.6-603.6; 305)	465.1±41.9 (187)	436.9±55.8 (115)	379.2 (1)	453.5±58.1 (92)	451.9±49.1 (125)	455.6±51.3 (281)	—	453.0±63.6 (69)	451.9±49.1 (125)	451.9±40.5 (24)	379.2 (1)	455.1±38.2 (23)
Ommastrephes bartrami	498.4±54.0 (287.8-589.6; 49)	491.9±54.5 (33)	511.8±52.3 (16)		505.1±71.4 (17)	496.4±44.5 (18)	405.6±39.6 (49)	—	505.1±71.4 (17)	496.4±44.5 (18)	—	—	—
Todarodes fillapovae#	446.6±50.8 (188.0-582.8; 1085)	449.0±55.3 (634)	443.1±43.5 (451)	447.3±76.2 (10)	450.8±48.5 (407)	441.7±54.7 (424)	446.2±50.4 (1063)	—	—	—	462.7±67.3 (22)	—	—
Kondakovia longimana	419.2±124.4 (169.0-914.9; 518)	386.1±111.4 (196)	439.3±127.7 (322)	320.1±108.5 (6)	433.0±138.4 (135)	419.5±114.9 (222)	417.7±123.2 (494)	—	423.8±137.5 (117)	419.5±114.9 (222)	449.5±146.6 (24)	320.1±108.5 (6)	492.7±133.2 (18)
Moroteuthis 'A'/ingens	424.2±51.2 (120.3-497.6; 113)	429.5±51.5 (73)	414.4±49.7 (40)	—	413.4±50.8 (41)	429.2±57.6 (52)	423.3±52.8 (99)	—	404.6±54.7 (27)	429.2±57.6 (52)	430.5±38.4 (14)	—	430.5±38.4 (14)
Moroteuthis knipovitchi	149.3±59.3 (-52.5-474.0; 314)	151.3±70.0 (153)	147.4±43.0 (161)	—	139.3±53.5 (65)	152.7±62.3 (196)	149.3±59.4 (312)	—	138.9±53.9 (63)	152.7±62.3 (196)	152.8±52.1 (2)	—	152.8±52.1 (2)
Moroteuthis lonnbergii	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Moroteuthis robsoni	732.3±185.1 (56.9-1204.8; 1227)	694.1±208.3 (426)	752.6±168.2 (801)	—	713.2±193.3 (630)	768.9±161.3 (481)	728.1±188.6 (1105)	—	699.5±200.9 (508)	768.9±161.3 (481)	770.4±144.9 (122)	—	770.4±144.9 (122)
Pholidoteuthis adami	198.8±46.6 (126.4-307.2; 14)	201.7±56.2 (9)	193.7±25.9 (5)	—	191.4±37.4 (12)	243.5±90.1 (2)	198.8±46.6 (14)	—	191.4±37.4 (12)	243.5±90.1 (2)	—	—	—
Pholidoteuthis boschmai	413.2±69.9 (233.2-755.0; 2131)	410.9±81.5 (809)	414.7±61.8 (1322)	—	416.1±64.0 (942)	411.0±68.6 (899)	412.2±70.9 (2027)	—	414.1±65.9 (838)	411.0±68.6 (899)	432.3±43.6 (104)	—	432.3±43.6 (104)
Vampyroteuthis infernalis	90.3±19.4 (43.8-125.0; 20)	85.6±18.2 (16)	109.0±11.6 (4)	—	88.2±23.6 (9)	91.1±16.5 (9)	88.4±18.0 (19)	—	83.6±20.5 (8)	91.1±16.5 (9)	125.0 (1)	—	125.0 (1)

^regression derived from Lu and Williams 1994
#regression derived from Lu and Ickeringill 2002
all other regressions derived from Clarke 1986

While differences were observed in the size of prey consumed between individuals in age group two and three, it is probable that these differences are highly influenced by the high variability observed in the diet of individuals and possible separation of foraging habitats between sexes (all males were in age group two). Of those prey species for which differences were observed between age groups, neither age group contained a higher proportion of larger cephalopod prey sizes, suggesting high individual variability within age groups.

6.4.2.4. Cephalopod species ecotype and tissue composition

The high species diversity of cephalopods observed in the diet of individuals in this study and the wide range of ecotypes these species have been recorded from suggest that large scale movements are undertaken by female groups of sperm whales. Female sperm whales are known to range large distances of at least 600x600 nautical miles from equatorial waters to around 40°S (Rice 1989; Jaquet *et al.* 2000). Marking programs around Australia have reported sperm whales of both sexes moving between the eastern Indian Ocean and south west Pacific, across southern Australia and also between eastern Australia and New Zealand (Brown 1981). Movements of sperm whales in search of food are thought to be in the order of 55 nautical miles per day (Jaquet *et al.* 2000).

The presence of cephalopod species from tropical to Antarctic regions therefore also represents movements over considerable temporal scales. There are few data on the passage rates and retention of the hard part remains of cephalopods. Clarke (1980) reported that an average female sperm whale would retain cephalopod beaks for 2.1 to 2.5 days while males would retain beaks for 1.2 to 1.6 days. Captive bottlenose dolphins (*Tursiops truncatus*) were observed to retain cephalopod beaks for up to 3 days (Ross 1979). The presence of cephalopod species described from tropical and Antarctic regions in the diet of individual sperm whales suggests that cephalopod beaks may be retained for longer periods than previously thought and may represent the diet of individuals over longer temporal scales.

Table 6.9: Calculated mean wet weights ±SD (n) in gm of cephalopod species in the stomach contents of sperm whales from Tasmania (range of wet wts included with n for all samples).

Species	Overall (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Haliphron atlanticus	1012.9±856.4 (404.7-3532.0; 12)	2066.9±1274.2 (3)	661.5±216.9 (9)	—	1091.2±923.4 (10)	—	1114.4±908.6 (10)	—	1237.6±985.3 (8)	—	505.4±142.5 (2)	—	505.4±142.5 (2)
Ancistrocheirus lesueuri	1241.1±1105.1 (95.5-10952.6; 1043)	1157.3±733.0 (501)	1318.7± 1357.7 (542)	1257.9±399.6 (2)	989.9±599.3 (354)	1186.6±931.2 (447)	1244.6± 1110.9 (1029)	—	991.6±603.0 (342)	1186.6±931.2 (447)	984.4±489.2 (14)	1257.9±399.6 (2)	938.8±502.4 (12)
Architeuthis sp.	21486.6±23580.4 (200.2-110233.1; 215)	21439.8± 23519.1 (191)	21858.8± 24574.8 (24)		18107.9± 21351.7(61)	21251.6± 23678.2 (102)	21226.1± 23323.4 (214)	—	991.6± 20083.8 (60)	21251.6± 23678.2 (102)	77244.32 (1)	—	77244.3 (1)
Japetella sp.	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Chiroteuthis joubini	184.8±132.2 (16.3-2208.4; 316)	178.4±71.0 (221)	199.6±215.6 (95)	58.3 (1)	171.7±55.4 (60)	184.3±174.4 (147)	183.6±131.7 (314)	58.3 (1)	165.1±38.7 (58)	184.3±174.4 (147)	365.7±134.7 (2)	—	365.7±134.7 (2)
Chiroteuthis veryani	151.7±149.8 (21.4-2697.3; 1361)	133.9±36.0 (697)	170.4±209.7 (664)	151.5±151.3 (1327)	137.5±37.9 (60)	169.8±216.7 (617)	151.5±151.3 (1327)	—	136.5±37.6 (456)	169.8±216.7 (617)	161.0±67.1 (34)	465.3 (1)	151.8±40.7 (33)
Chiroteuthis sp.	252.7±117.8 (60.6-465.3; 15)	231.5±33.9 (3)	258.0±131.6 (12)	—	271.0±117.3 (12)	179.8±107.8 (3)	237.6±106.0 (14)	—	253.3±104.9 (11)	179.8±107.8 (3)	465.3 (1)	—	465.3 (1)
Chtenopteryx sp.?	19.7 (1)	19.7 (1)	—	—	—	19.7 (1)	19.7 (1)	—		19.7 (1)	—	—	—
Cranchia scabra	43.8±11.4 (17.9-75.3; 60)	38.6±10.4 (15)	45.5±11.4 (45)	—	38.5±9.3 (23)	51.2±10.8 (19)	43.8±11.4 (60)	—	38.5±9.3 (23)	51.2±10.8 (19)	—	—	—
Galiteuthis glacialis	73.2±23.5 (2.7-338.8; 1279)	78.2±25.7 (411)	70.8±22.0 (868)	46.9±13.4 (4)	71.1±25.9 (523)	71.6±20.5 (545)	73.0±22.3 (1263)	32.0 (1)	70.4±23.1 (510)	71.6±20.5 (545)	87.9±70.7 (16)	51.9±10.9 (3)	96.2±76.3 (13)
Galiteuthis pacifica	49.5±19.5 (26.9-75.2; 5)	49.9±22.5 (4)	47.7 (1)	—	61.6±13.7 (3)	31.3±6.1 (2)	49.5±19.5 (5)	—	61.6±13.7 (3)	31.3±6.1 (2)	—	—	—
Megalochranchia sp.	360.3±227.5 (48.1-1616.7; 214)	417.4±293.3 (56)	340.1±196.2 (158)	—	428.2±282.0 (73)	327.8±201.7 (103)	360.3±227.5 (214)	—	428.2±282.0 (73)	327.8±201.7 (103)	—	—	—
Mesonychoteuthis hamiltoni	916.9±991.6 (22.6-7000.0; 770)	838.4±810.3 (264)	957.9±1072.7 (506)	423.6±175.3 (24)	986.7±1024.5 (309)	896.0±1028.6 (351)	853.5±947.7 (672)	—	813.3±901.3 (213)	896.0±1028.6 (351)	1352.2± 1167.6 (98)	423.6±175.3 (2)	1371.6±1171.8 (96)
Taonius pavo	260.1±64.1 (88.2-593.7; 932)	255.8±64.9 (709)	273.7±59.6 (223)	303.8 (1)	255.9±61.2 (310)	255.9±64.2 (481)	259.5±64.2 (915)	—	254.3±61.1 (294)	255.9±64.2 (481)	287.3±55.2 (17)	303.8 (1)	255.9±61.2 (310)
Teuthowenia pellucida	228.9±51.1 (36.3-411.8; 822)	224.4±53.9 (439)	234.0±47.3 (383)	294.0±46.7 (2)	219.7±53.5 (265)	230.2±51.5 (392)	228.7±51.2 (810)	—	219.1±54.0 (255)	230.2±51.5 (392)	236.3±50.1 (12_	294.0±46.7 (2)	234.1±37.1 (10)
Cycloteuthis akimushkini	347.9±139.1 (141.0-429.7; 4)	141.0 (1)	416.9±22.3 (30	—	—	416.9±22.3 (3)	347.9±139.1 (4)	—	416.9±22.3 (3)	—	—	—	—
Discoteuthis discus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Table 6.9 continued.

Species	Overall (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Gonatus antarcticus	320.5±90.7 (125.8-573.5; 59)	316.3±93.3 (46)	335.2±82.7 (13)	—	313.9±96.6 (24)	31.3±6.1 (2)	317.6±88.8 (58)	—	306.4±91.4 (23)	342.7±87.5 (27)	485.5 (1)	—	485.5 (1)
Histioteuthis A1	199.1±44.4 (86.7-331.0; 65)	199.1±44.4 (65)	—	—	—	199.0±42.7 (59)	199.1±44.4 (65)	—	—	199.0±42.7 (59)	—	—	—
Histioteuthis macrohista	144.8±69.3 (34.4-313.2; 275)	66.1±13.8 (64)	168.6±61.3 (211)	73.5 (1)	128.3±71.5 (69)	157.4±65.8 (190)	145.1±69.2 (274)	73.5 (1)	129.5±71.3 (68)	157.4±65.8 (190)	46.9 (1)	—	46.9 (1)
Histioteuthis melaegroteuthis	60.0±11.3 (31.6-138.7; 317)	59.4±7.1 (103)	60.2±12.9 (214)	—	59.3±8.4 (117)	62.3±13.7 (128)	60.0±11.4 (310)	—	59.4±8.5 (110)	62.3±13.7 (128)	57.2±6.3 (7)	—	57.2±6.3 (7)
Histioteuthis bonnelli	196.9±39.9 (43.6-412.4; 2524)	201.0±43.6 (947)	194.5±37.3 (1577)	169.8±30.2 (9)	197.9±39.7 (885)	193.9±41.3 (1194)	197.0±39.9 (2501)	—	197.9±39.8 (871)	193.9±41.3 (1194)	186.8±35.0 (23)	169.8±30.2 (9)	197.8±34.3 (14)
Histioteuthis celetaria pacifica	259.7±93.8 (65.3-479.6; 16)	244.9±95.9 (8)	274.4±95.8 (8)	—	301.0±126.4 (4)	273.0±63.8 (9)	245.9±82.6 (12)	—	—	273.0±63.8 (9)	301.0±126.4 (4)	—	301.0±126.4 (4)
Histioteuthis miranda	575.8±127.2 (208.9-1166.2; 510)	574.6±122.6 (183)	576.4±129.8 (327)	490.4 (2)	558.4±130.9 (191)	564.2±112.8 (208)	575.6±125.7 (501)	—	556.4±126.6 (184)	564.3±112.8 (208)	584.0±202.2 (9)	490.4±0.0 (2)	610.8±225.3 (7)
Histioteuthis hoylei	327.8±99.3 (87.1-859.9; 968)	334.2±97.8 (419)	323.0±100.3 (549)	324.7±91.5 (2)	328.7±93.1 (437)	309.5±99.2 (338)	327.9±99.6 (940)	—	329.0±93.0 (411)	308.9±98.6 (337)	324.7±91.5 (28)	335.1±27.7 (2)	323.9±94.9 (26)
Histioteuthis sp. Type A (1)	230.0±63.4 (65.3-377.4; 158)	228.1±61.8 (139)	244.9±74.1 (19)	—	240.9±67.2 (56)	215.0±52.9 (83)	230.1±63.4 (158)	—	240.9±67.2 (56)	215.0±52.9 (83)	—	—	—
Histioteuthis B1	191.9±44.9 (53.9-340.0; 1259)	191.3±42.7 (1149)	198.7±63.9 (110)	—	179.6±51.2 (159)	197.3±41.0 (837)	191.6±45.0 (1245)	—	175.9±51.4 (145)	197.3±41.0 (837)	218.1±29.3 (14)	—	218.1±29.3 (14)
Histioteuthis eltaninae	132.5±17.8 (46.9-239.5; 1810)	132.4±18.6 (566)	132.5±17.5 (1244)	—	131.9±17.7 (566)	132.8±18.0 (965)	132.5±17.9 (1785)	—	131.7±17.9 (541)	132.8±18.0 (965)	136.2±12.9 (25)	—	136.212.9 (25)
Histioteuthis B2	165.7±43.7 (37.4-389.0; 6186)	174.6±42.6 (3755)	152.0±41.8 (2431)	169.2 (1)	167.3±45.9 (2150)	165.4±42.2 (3246)	165.7±43.8 (6088)	—	167.2±46.2 (2053)	165.4±42.2 (3246)	168.4±38.6 (98)	169.2 (1)	168.4±38.8 (97)
Histioteuthis reversa	141.9±27.5 (73.5-224.5; 345)	145.4±25.9 (123)	139.9±28.2 (222)	140.3±19.1 (5)	142.7±28.3 (251)	139.3±26.6 (81)	142.5±27.4 (316)	—	143.6±28.1 (227)	139.3±26.6 (81)	135.6±27.9 (29)	140.3±19.1 (5)	134.6±29.6 (24)
Histioteuthis atlantica	168.8±43.3 (57.6-401.9; 4635)	169.2±39.5 (2916)	168.1±49.1 (1719)	179.6±33.4 (9)	173.5±48.0 (1554)	167.0±40.7 (2466)	168.7±43.5 (4435)	—	173.6±49.2 (1363)	167.0±40.7 (2466)	172.5±38.4 (200)	158.1±54.1 (3)	172.7±38.3 (197)
Histioteuthis B4	176.2±41.9 (37.4-389.0; 7011)	175.9±40.9 (5333)	177.2±45.1 (1678)	156.0±32.7 (21)	179.4±43.8 (2065)	173.6±40.6 (3718)	176.2±42.1 (6653)	143.5±36.8 (11)	180.2±44.5 (1717)	173.6±40.6 (3718)	175.2±39.8 (358)	169.8±21.6 (10)	175.4±40.2 (348)
Histioteuthis sp. Type B(1)	212.8±53.2 (73.5-313.2; 168)	211.2±56.7 (113)	215.9±45.6 (55)	—	232.9±45.6 (57)	213.9±44.2 (50)	212.8±53.2 (168)	213.9±44.2 (50)	—	—	—	—	—
Histioteuthis sp. Type B(2)	184.9±45.0 (86.7-304.5; 281)	190.7±44.7 (159)	177.3±44.4 (122)	—	197.5±45.6 (112)	177.1±41.5 (115)	184.8±45.9 (261)	—	200.0±47.7 (92)	177.1±41.5 (115)	185.7±32.4 (20)	—	185.7±32.4 (20)
Lepidoteuthis grimaldi	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Idioteuthis cordiformis	279.6±135.9 (65.1-1398.1; 442)	245.5±90.6 (171)	301.1±154.3 (271)	340.0 (1)	290.5±143.3 (169)	279.0±113.5 (173)	280.0±137.5 (418)	—	293.9±148.1 (146)	279.0±113.5 (173)	271.7±107.3 (24)	340.0 (1)	268.7±108.7 (23)

Table 6.9 continued.

Species	Overall (N=36)	STR1 (N=15)	STR2 (N=21)	Age grp1 (N=2)	Age grp2 (N=14)	Age grp3 (N=15)	All Female (N=30)	Female Age grp1 (N=1)	Female Age grp 2 (N=9)	Female Age grp 3 (N=15)	All Male (N=6)	Male Age grp 1 (N=1)	Male Age grp 2 (N=5)
Mastigoteuthis psychrophile	25.8±6.3 (20.7-32.8; 3)	22.2±2.2 (2)	32.8 (1)	—	25.7±6.3 (3)		25.7±6.3 (3)	—	—	25.7±6.3 (3)	—	—	—
Mastigoteuthis sp.	112.4±52.9 (37.4-263.7; 25)	98.0±41.0 (2)	120.5±58.3 (16)	—	139.2±17.0 (4)	107.3±60.3 (18)	111.6±53.9 (24)	—	141.8±19.8 (3)	107.3±60.3 (18)	131.1 (1)	—	131.1 (1)
Octopoteuthis rugosa	313.9±175.0 (92.3-1389.3; 709)	349.6±198.1 (403)	267.5±126.8 (285)	—	303.4±154.9 (260)	310.9±157.0 (328)	313.6±175.7 (673)	—	300.6±153.7 (224)	310.9±157.0 (328)	320.6±163.5 (36)	—	320.6±163.5 (36)
Taningia danae	6107.2±4115.6 (708.9-19516.2; 278)	5864.2± 4157.2 (215)	6936.5± 3888.6 (63)		6115.6± 3898.7 (88)	5973.1± 4222.5 (158)	6069.6± 4153.8 (268)	—	5987.5± 4007.3 (78)	5973.1± 4222.5 (158)	7114.4± 2879.4 (10)	—	7114.4± 2879.4 (10)
Nototodarus gouldi	2911.0±895.4 (250.9-4997.2; 305)	3123.3±796.9 (190)	2560.4±941.3 (15)	1509.1 (1)	2811.0±870.4 (92)	2876.7±939.4 (125)	2916.2±907.8 (281)	—	2779.0±920.1 (69)	2876.7±939.4 (125)	2850.1±748.4 (24)	1537.0 (1)	2907.1±709.7 (23)
Ommastrephes bartrami	2810.7±681.8 (720.1-4137.4; 49)	2724.1±662.5 (33)	2989.1±707.6 (16)	—	2935.5±845.7 (17)	2765.7±587.6 (18)	2810.7±681.8 (49(	—	2935.5±845.7 (17)	2765.7±587.6 (18)	—	—	—
Todarodes fillapovae	2075.9±669.4 (115.0-4901.2; 1085)	2194.4±715.2 (634)	1909.3±558.9 (451)	2403.1±733.5 (4)	2024.9±633.7 (413)	2179.5±734.2 (424)	2072.5±667.9 (1063)	2008.9±682.2 (2)	2016.9±628.4 (393)	2179.5±734.2 (424)	2237.7±735.3 (22)	2797.3±725.9 (2)	2181.7±730.5 (20)
Kondakovia longimana	1782.7±2438.2 (21.5-30729.1; 518)	1211.6± 1818.2 (196)	213.0±2691.8 (322)	533.4±703.8 (6)	2220.2± 3302.4 (135)	1776.0± 1924.7 (222)	1744.7± 2404.6 (494)	—	2062.7± 3306.0 (117)	1776.0± 1924.7 (222)	2566.2± 3002.6 (24)	533.4±703.8 (6)	3243.8± 3179.3 (18)
Moroteuthis 'A'ingens	2085.9±576.7 (51.6-3227.4; 113)	2168.4±510.8 (73)	1935.3±661.5 (40)	—	1931.6±632.6 (41)	2182.4±586.5 (52)	2078.8±584.6 (99)	—	1825.5±661.9 (27)	2182.4±586.5 (52)	2136.3±535.3 (14)	—	2136.3±535.3 (14)
Moroteuthis knipovitchi	267.7±148.6 (43.7-1438.3; 314)	279.7±193.4 (153)	256.4±86.1 (161)	—	241.7±97.7 (65)	274.6±169.4 (196)	267.7±149.0 (312)	—	240.7±98.4 (63)	274.6±169.4 (196)	273.9±94.1 (2)	—	273.9±94.1 (2)
Moroteuthis lonnbergii	615.8±212.4 (67.7-1183.6; 204)	716.7±203.7 (90)	536.2±184.0 (114)	—	533.6±187.2 (84)	639.2±191.9 (74)	622.1±213.9 (190)	—	534.2±190.5 (70)	639.2±191.9 (74)	530.4±175.8 (14)	—	530.4±175.8 (14)
Moroteuthis robsoni	8604.8±6806.1 (27.5-64046.9; 1287)	8931.2± 7923.2 (487)	8398.4± 6022.5 (801)	7443.0± 5415.7 (9)	7947.9± 5936.6 (587)	9884.4± 7823.6 (482)	8513.6± 6980.0 (1112)	—	7423.1± 5863.7 (421)	9889.7± 7830.9(481)	9184.5± 5558.2 (175)	7443.0± 5415.7 (9)	9278.9± 5566.1 (166)
Pholidoteuthis adami	225.4±173.5 (48.9-708.2; 14)	246.2±211.2 (9)	187.9±76.8 (5)	—	191.9±112.2 (12)	426.0±399.0 (2)	225.4±173.5 (14)	—	191.9±112.2 (12)	426.0±399.0 (2)	—	—	—
Pholidoteuthis boschmai	1823.1±973.0 (313.7-9618.4; 2131)	1842.0± 1127.3 (809)	1811.6±865.5 (1322)		1838.0±890.0 (942)	1789.3±938.4 (899)	1813.2±985.4 (2027)	—	1816.0±922.9 (838)	1789.3±938.4 (899)	2015.6±664.8 (104)	—	2015.6±664.8 (104)
Vampyroteuthis infernalis	431.3±275.7 (31.3-1142.6; 20)	356.2±222.4 (16)	731.9±288.9 (4)	—	428.1±340.9 (9)	421.9±223.7 (9)	393.9±225.0 (19)	—	338.8±225.2 (8)	421.9±223.7 (9)	1142.6 (1)	—	1142.6 (1)

^regression derived from Rodhouse *et al.* 1990
#regression derived from Lu and Ickeringill 2002
all other regressions derived from Clarke 1986
Note: regression was not available for *L. grimaldi*.

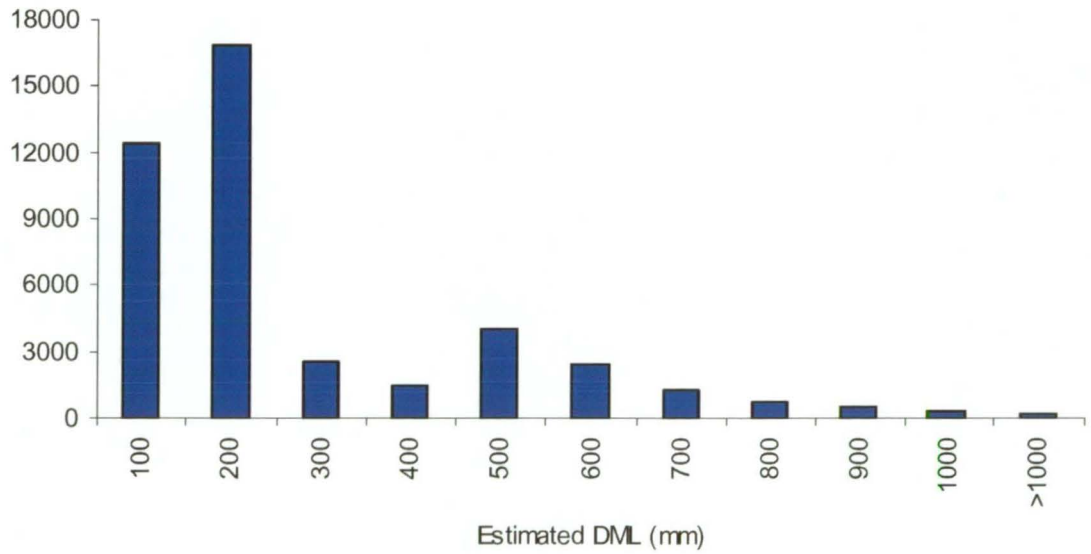


Figure 6.4: Distribution of the dorsal mantle lengths of cephalopod prey in the diet of southern Australian sperm whales.

While differences in the numerical abundance of species on the basis of ecotypes were found between stranding sites and sexes, there were no differences in the percentage weight contributed to diet by species from each of the ecotypes. It is probable that those differences observed in the numerical abundance of species are the result of high individual variability in prey items encountered rather than a separation of foraging habitat between individuals in each stranding group or between males and females. The results presented here suggest that while the sperm whales in this study range across a diverse number of ecotypes, the highest proportion of foraging occurs in subtropical regions.

The presence of the Antarctic species *Galiteuthis glacialis*, *G. antarcticus*, *K. longimana*, *M. psychrophila* and *Moroteuthis knipovitchi* in the diet of female and immature sperm whales may be the result of (i) the redistribution of prey species northwards as a result of oceanographic conditions or (ii) movement of female groups of sperm whales further south than are generally considered to occur. A number of subantarctic and Antarctic species of cephalopods have been recorded north of their usual range in association with northwardly moving cold water currents (Nesis 1972; Imber 1978; Alexeyev 1994). Often frontal systems such as the sub-tropical and subantarctic convergences serve as boundaries to the distribution of cephalopod species (Clarke 1980; Voss 1985; Rodhouse *et al.* 1992; Dunning 1993). Rather than being stable, non-moving boundaries, these are dynamic, moving their geographic position continuously depending on both broad-scale and localized oceanographic conditions. Consequently, species associated with these boundaries also redefine their distributions. Frontal system movements may have redistributed these Antarctic species into those areas utilized by female sperm whales. Clarke and MacLeod (1982) also reported *K. longimana* from female sperm whales caught in the Tasman Sea and suggested that the distribution of this species could be further north than previously thought. They additionally suggested that female sperm whales may range further south than previously reported. Female sperm whales around the New Zealand region have been reported to occur regularly in waters down to 50°S (Gaskin 1973). This may also occur in the southeast Australian region. Investigations into the movements of female sperm whales and cephalopod species in this region would provide greater insights into possible reasons for the presence of such species in the diet of sperm whales.

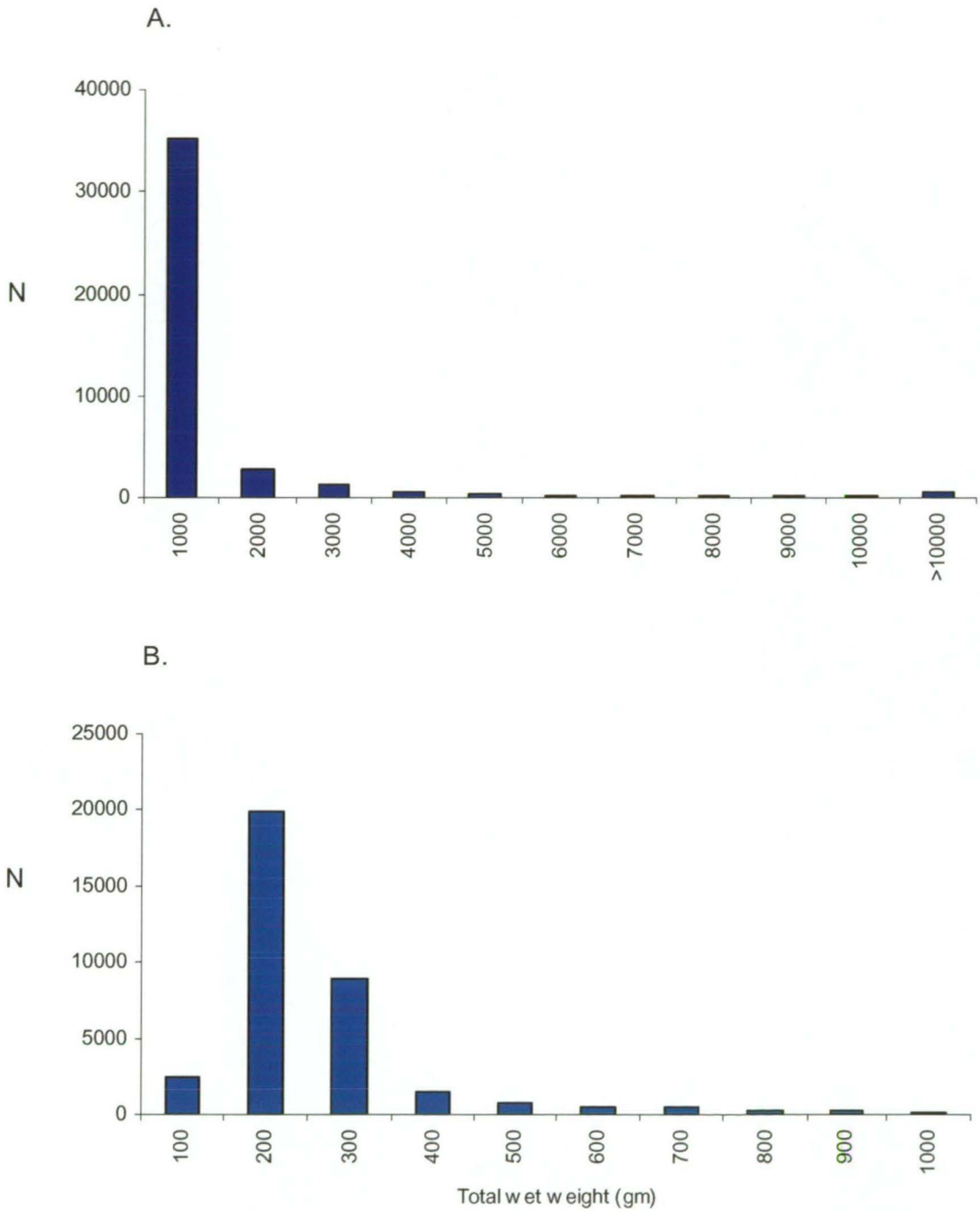


Figure 6.5: Distribution of the estimated wet weights of cephalopod prey in the diet of southern Australian sperm whales (a): all estimated wet weights; (b): estimated wet weights less than 1,000 gm only.

The diet of sperm whales observed in this study was predominantly composed of muscular cephalopods. While a comprehensive data on the calorific content of cephalopod species is lacking, those assessments that have been undertaken demonstrate cephalopods to be an appreciably lower source of energy to top predators than fish or crustaceans (Croxall and Prince 1982). Within the cephalopod group, muscular species demonstrate higher calorific content than gelatinous species (Clarke *et al.* 1985). For a large predator such as the sperm whale which needs to consume 3-4 % of its body mass per day (Lockyer 1981b), the higher calorific content of muscular cephalopods is likely to be of importance and thus results in a predominance of muscular cephalopods in the diet of these animals.

Adult female and pubertal male sperm whales have been tracked diving to depths of 900 m, while immature sperm whales have been recorded to depths of 700 m (Lockyer 1977). However, the majority of dives in all animals were to depths less than 400 m. The cephalopod species represented in the diet of the sperm whales in this study are reported to range throughout the water column to depths of 3,000 m (Table 6.7). All excepting *V. infernalis* also occur in waters less than 500 m, suggesting that at least the sperm whales in this study may spend a large amount of time foraging in depths of less than 500 m.

Table 6.10: Cephalopod species for which LRLs differed significantly between stranding site and age groups.

Site (d.f.=2)			Age (d.f.=1)		
Species	F-ratio	*P*	Species	F-ratio	*P*
Architeuthis sp.	4.3	0.02	*C. scabra*	6.4	0.02
C. v. veryanii	5.9	0.003	*G. glacialis*	14.3	0.0002
H. macrohista	76.0	0.0001	*H. macrohista*	18.4	0.0001
H. bonnelli	9.1	0.003	*H. bonnelli*	9.1	0.003
Histioteuthis sp. A(1)	13.8	0.0001	*H. hoylei*	9.1	0.003
Histioteuthis B1	8.1	0.0003	*Histioteuthis* sp. A(1)	5.6	0.02
Histioteuthis B2	312.7	0.0001	*Histioteuthis* B1	44.3	0.0001
H. atlantica	32.4	0.0001	*Histioteuthis* B4	14.8	0.0001
Histioteuthis B4	9.0	0.0001	*Histioteuthis* sp. B(1)	4.3	0.04
Histioteuthis sp. B(2)	8.6	0.0003	*Histioteuthis* sp. B(2)	12.1	0.001
I. cordiformis	15.9	0.0001	*K. longimana*	8.4	0.004
L. grimaldi	75.3	0.0001	*L. grimaldi*	30.4	0.0001
M. hamiltoni	4.4	0.01	*M. ingens*	3.9	0.05
M. lonnbergii	14.4	0.0001	*M. lonnbergii*	14.7	0.0002
M. robsoni	8.6	0.0002	*M. robsoni*	40.2	0.0001
N. gouldi	14.4	0.0001	*T. pellucida*	6.5	0.01
O. rugosa	33.5	0.0001			
P. boschmai	8.0	0.0004			
T. pavo	5.3	0.005			
T. fillapovae	36.6	0.0001			

6.4.3. The diet of sperm whales in relation to fisheries in this region

The commercial harvest of cephalopods in this area has been in operation periodically since 1972, targeting the Ommastrephids *N. gouldi, T. filippovae* and *O. bartrami* and the Sepioteuthid *Sepioteuthis australis*. Fishery effort has varied throughout this time with foreign fishing vessels taking up to 7,914 tonnes during the 1970s, while current domestic catches have increased from 439 to 1,673 tonnes per season between 1995/96 to 1997/98 (AFMA 2001). While *S. australis* was not present in the diet of sperm whales in this study, all of the Ommastrephids targeted by the fishery were, comprising 3.9 % of the diet numerically and 9.6 % by weight. If it is assumed that sperm whales consume 3.5 % of their total mass per day (Lockyer 1981b), then after calculating total weight (W_t=0.006648$L_m^{3.18}$, Lockyer 1981b) of all individuals involved in the Tasmanian strandings (see Chapter Two), the total mass of Ommastrephids consumed by this subsample of the total population in southern Australian waters is in the order of 40.1 tonnes per day, far greater than the current fishery operations in the area. Further information on the diet of sperm whales during other times of the year coupled with information on the distribution and population numbers throughout this region is important in order to understand any potential competition, the distribution of this competition temporally and spatially and the impacts of such competition on cephalopod populations in this area.

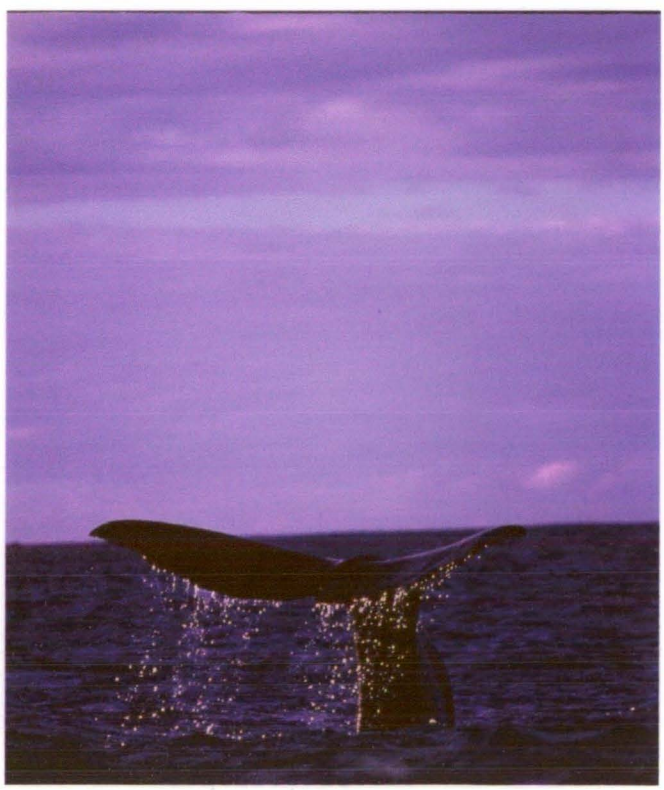
6.5. SUMMARY

- The diet of predominantly female groups of sperm whales from two mass strandings in Tasmania, Australia was investigated from hard part remains. Dietary assessments were conducted between stranding groups, sex and age groups.
- Stomach contents were dominated by oceanic species of cephalopods representing 48 species from 14 families of Teuthids, two species from two families of Octopods and the single Vampyromorph species.
- Species diversity was higher than that reported previously in the Southern Hemisphere and dietary composition was dominated by species from the Histioteuthidae, Ommastrephidae, Onychoteuthidae, Cranchiidae and Pholidoteuthidae families.
- Cephalopods less than 300 mm dorsal mantle length dominated the diet numerically, while those greater than 1,000 gm comprised 78.6% of the estimated wet mass, highlighting the importance of larger cephalopod species in the efficient acquisition of energy.
- The two stranding groups appeared to be comprised of a number of foraging groups, possibly based on social units, which had been foraging in different areas prior to the strandings.
- There was some evidence of segregation of foraging groups on the basis of gender and age, although it was difficult to separate the two factors.
- High individual variation characterized the diet of these sperm whales.

Evans, K, Hindell, M. A. and D. Thiele. (2003) Body fat and condition in sperm whales, Physeter macrocephalus, from southern Australian waters. Comparative Biochemistry and Physiology. Part A: Molecular and Integrative Physiology 134:847-862.

SECTION FOUR

HUMAN IMPACTS ON SPERM WHALES IN SOUTHERN AUSTRALIAN WATERS: POLLUTANTS



CHAPTER EIGHT

CONCENTRATIONS OF ORGANOCHLORINES IN SPERM WHALES, *Physeter macrocephalus*, FROM SOUTHERN AUSTRALIAN WATERS[1].

8.1. INTRODUCTION

Pollution is one of a number of contemporary environmental problems that face marine mammals (Johnston *et al.* 1996). While the majority of man-made toxic compounds are no longer produced in most developed countries, they are still produced in developing nations and are in use globally (Tanabe *et al.* 1994; Simonich and Hites 1995). Many of these pollutants, particularly the organochlorines, are characterized by their chemical stability and resistance to metabolic degradation. As a result, they are readily taken up into food webs and accumulate with increasing trophic levels. Organochlorines are transported globally as a function of atmospheric circulation, primarily involving movement from low latitudes to high latitudes, with the open ocean serving as their ultimate repository (Iwata *et al.* 1993, Tanabe *et al.* 1983). Their resilience and this form of transportation suggest that at least in the near future, levels will not decline, but may eventually reach a global equilibrium (Wania and Mackay 1995) as pollutants move away from source points. This has consequences for those areas that are removed from the sources of pollutant production and in the past have been characterized by low pollutant concentrations, such as the high latitudes and the Southern Hemisphere in general.

Some cetacean species bioaccumulate organochlorine pollutants as a result of their longevity, location towards the top of the food chain, the ability of their blubber layer to store up to 90 % of whole body burdens and their limited ability to metabolize many of these compounds (Tanabe *et al.* 1981; 1988; Jepson *et al.* 1999). Of these compounds, the polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT) and its metabolites dichlorodiphenyldichloroethylene (DDE) and dichlorodiphenyldichloroethane (DDD) present the largest problem to marine mammals

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(Borrell and Aguilar 1993; Reijnders 1994). These organochlorines have been associated with deleterious effects on the immune, endocrine and nervous systems of pinnipeds and cetaceans, resulting in disruption in growth, development, reproductive impairment and resistance to disease (Béland *et al.* 1993; Reijnders 1994; Reijnders and Ruiter-Dijkman 1995; Ross *et al.* 1996; Skaare *et al.* 2000). Deleterious effects on the immune system and subsequent lowering of the ability to resist disease have been suggested as possible factors involved in mass mortality events and strandings (Aguilar and Borrell 1994a; Joiris *et al.* 1997; Jepson *et al.* 1999; Tilbury *et al.* 1999). However, directly associating contaminant concentrations and toxicity is difficult due to a number of confounding factors. Age, sex, the diet and condition of an individual, individual and species-specific ability to metabolize and excrete pollutants all have considerable effects on concentrations (Evans In Press). Many samples used in pollutant studies have been derived from single strandings, bycaught animals or animals harvested in whaling operations. For a large proportion of single-stranded animals, the cause of death is unknown but may be associated with disease. Consequently, concentrations of pollutants in these samples may not reflect that of the healthy population (Aguilar *et al.* 1999). Sex ratios and age structure are often biased in bycaught animals and those from the whaling industry, thereby hampering the identification of patterns of pollutant concentrations throughout populations. Mass-stranded animals are thought to be largely free of biases associated with disease and therefore represent the best source of unbiased, comprehensive samples. However, pollutant studies utilizing mass-stranded animals (other than those associated with viral epidemics) are sparse.

Oceanic species of cetaceans such as sperm whales (*Physeter macrocephalus*), as part of open ocean ecosystems distanced from point sources of pollutants, can be regarded as removed from the short term changes in pollutant concentrations typical of inshore areas (Aguilar 1985; Reijnders 1986). Female sperm whales are distributed in waters from the equator to around 40°S (Rice 1989), with individual groups ranging throughout areas in the order of 600x600 nautical miles. Within this area, they may move up to 55 nautical miles per day searching for food (Jaquet *et al.* 2000). Differences in the chemical profiles and concentrations of pollutants in different water masses should be reflected in the pollutant load of animals that feed in those areas (Aguilar 1987; Aguilar *et al.* 1993). Therefore, concentrations of organochlorine compounds in sperm whales should be reflective of broad scale regional oceanic levels of pollution unbiased by variable, localised concentrations of pollutants close to point sources.

Three mass strandings of sperm whales on the west and north coasts of Tasmania, Australia in 1998 provided a unique opportunity to investigate (i) levels of organochlorines within this species, thereby contributing to the sparse documentation of these compounds in this region; (ii) variation in the levels of these compounds with age and sex as well as between stranding groups; (iii) the relationship between blubber lipid content and concentrations of compounds in this species and (iv) possible stratification of organochlorines within the blubber across females and males and the implications of any stratification to inter-study comparisons in this species.

8.2. MATERIALS AND METHODS

8.2.1. Sample collection

Samples (n=37) of 50-100 gm blubber encompassing the complete depth were collected from individuals involved in two mass strandings in February 1998 (STR1: Ocean Beach, Strahan, n=25 and STR2: Greens Pt. Beach Marrawah, n=12). All samples were taken from the dorsal area in line with the posterior insertion of the flipper between 48-72 hours after death. All samples were wrapped in aluminium foil, stored in ice on site and then frozen at -20°C on return to the University of Tasmania.

The sex and total length of all animals [tip of upper jaw to deepest notch in fluke taken in a straight line dorsally (Norris 1961)] were recorded. Each individual was assigned an age based on counts of the number of growth layers in a tooth taken from that animal (Chapter Two; Chapter Three). Lactation status was determined by applying pressure to teats and through the identification of the presence of milk via dissecting mammary glands.

8.2.2. Sample analyses

8.2.2.1. Stratification of samples

The lipid content of the blubber of sperm whales has been found to vary with depth (Lockyer 1991; Chapter Seven). To investigate whether organochlorine concentrations followed the same stratification patterns as a consequence of their lipophillic nature, a subsample (n=10) of blubber samples from the Marrawah stranding encompassing the total depth of blubber were sectioned into three parts following Lockyer (1991). These were then treated as separate samples during analysis.

8.2.2.2. Extraction of lipid fraction of blubber

Subsamples of each blubber sample were cleaned (outer surfaces of the sample were removed) and approximately three grams (mean: 2.9±0.3 gm) were weighed to ±0.01 gm and roughly chopped into pieces with a scalpel. These were then ground in a mortar and pestle with anhydrous sodium sulphate and placed into a 125 mL Soxhlet apparatus to which 80 mL of *n*-hexane was added. The samples were left to extract for four hours. After extraction the beakers containing the extract and hexane were transferred to a hot water bath and evaporated to 40 mL. The extracts were then divided into two portions: 30 mL for pollutant analysis and ten mL to determine lipid content (Chapter Seven).

8.2.2.3. Determination of blubber lipid content

The ten mL extract was transferred to a previously tared vial and the solvent evaporated under a stream of N_2. After returning to room temperature, the vial was reweighed and the total lipid content of the sample determined by subtraction. Lipid content was expressed as a percentage of the wet weight of the tissue after accounting for the division of the extract.

8.2.2.4. Determination of organochlorine concentrations

Each 30 mL extract was cleaned using sulphuric acid following the procedures in Murphy (1972). After phase separation, the cleaned extract was concentrated to one mL and 100 µL of an internal standard (tetrachlorobenzene for the PCBs and deuterated PAH for the HCHs and DDTs) was added. Each extract was analysed for *p, p'*-DDT, *p, p'*-DDE, *p, p'*-DDD, α-HCH (benzene hexachloride, also known as hexachlorocyclohexane), β-HCH, γ-HCH (lindane) δ-HCH and the seven PCB congeners identified on the ICES primary list (CBs 28, 52, 101, 118, 138, 153 and 180).

For the identification and quantification of PCBs, each sample was injected into a Varian 3400 gas chromatograph with a 1079 split/splitless injector (injector temperature 290°C), equipped with an electron capture detector (temperature 300°C). The column was a Chrompack CP58-60 column of 0.25 mm internal diameter, 30 m length and a stationary phase CP-SIL 8 CB low bleed with a film thickness of 0.25 µm. Helium was used as the carrier gas and the injection volume was one µL with the injector operating in the splitless mode. Temperature was programmed according to the following sequence: injection at 60°C; oven held for the first minute and then increased by 10°C min^{-1} to 300°C. The oven was then held at this temperature for ten minutes. The autosampler used was a Varian 8200CX. PCB congeners were selected from those present in Aroclor

1254 based on their relative peak size and isolation from interfering peaks. PCBs in the samples were identified using individual congeners and quantified using congeners in Aroclor 1254 and additionally with individual congeners.

A Varian CP-3800 gas chromatograph with a 1079 split/splitless injector (injector temperature 290°C) and a Varian Saturn 2000 ion trap mass spectrometer were used for the identification and quantification of *p, p'*-DDT and it's metabolites and the four HCH isomers. The column was a J&W DB5MS column of 0.25 internal diameter, 30 m length and a stationary phase DB5 low bleed with a film thickness of 0.25 μm. Column temperature was initially 40°C and was increased at 10°C min^{-1} until it reached 290°C where it was held for eight minutes. There was a constant column flow of 1.0 ml min^{-1} and the autosampler used was a Varian 8200CX. Software used for data analysis and calculations was the Varian Saturn GC/MS workstation version 5.41. Detection limits were 0.1 μg mL^{-1}.

Standards containing the analytes of interest were prepared at concentrations of one, ten and 100 μg mL^{-1}. These were analysed at the same time as the samples and were used to quantify the analytes by relative retention times and mass spectral confirmation. Procedural blanks were included in each run during the course of analysis. Extraction efficiencies calculated by running a series of spiked samples for all analytes were above 85 %.

All materials used during the analytical process were cleaned between each sample to prevent cross-contamination. All concentrations are presented on the basis of the extractable lipid content of each sample. Presenting results on this basis accounts for at least part of the heterogeneity associated with the nutritive condition of the animals sampled and the methods used for lipid extraction (Aguilar *et al.* 2002).

We found during analysis that the PCB congener 138 co-eluted with *p, p'*-DDT, and although longer running times helped to separate out compounds, final concentrations were probably still biased to some degree by the co-elution. Consequently concentrations of this congener were not used in statistical analyses.

8.2.2.5. Statistical analyses

Probability plots were used to test data for normality and due to non-normality all organochlorine concentration data were log-transformed. The relationships between organochlorine concentrations on a wet weight basis and blubber lipid content were investigated via linear regression. Body mass is thought to influence pollutant levels in individuals (Aguilar *et al.* 1999). In order to investigate this relationship, length data were used to calculate estimates of weight for all individuals ($W_t=0.006648L_m^{3.18}$; Lockyer 1981b). Organochlorine concentrations were regressed against estimated weight and age to determine any possible relationships.

Because pollutants are known to accumulate in other cetaceans with age (Aguilar *et al.* 1999), it was important to account for possible age effects when testing for differences between groups of animals (*e.g.* stranding, sex). Differences between stranding groups were investigated using a multivariate general linear model (GLM) with age as a covariate. Similarities in concentrations between reproductive groups (non-lactating, lactating and immature females), age groups and sexes were tested using a one-way Analysis of Similarity (ANOSIM). Animals were assigned to age groups based on approximate maturity of individuals (Lockyer 1981b; Rice 1989). These corresponded to (1) juvenile or immature (female: $\leq$13 years; male: <19 years; n=5); (2) sexually mature but not physically mature (female: >13$\leq$30 years; male: $\geq$19$\leq$35 years; n=9) and (3) sexually and physically mature (female: >30 years; male: >35 years; n=20). Three animals were not aged and all males were less than 23 years.

Concentrations of organochlorines were compared between stranding groups via backwards stepwise discriminant function analysis (DFA) using a Wilke's Lambda method at the 95 % significance level.

To determine if pollutant concentrations were stratified with depth throughout the blubber layer, log- transformed data from the three strata were compared using a repeated measures ANOVA.

Where concentrations were presented as 'not detected' (ND) the midpoint between zero and the detection limit (0.1 $\mu g\ mL^{-1}$) was used for statistical analyses.

8.3. RESULTS

DDTs and PCBs were present in all of the 37 samples analysed (Tables 8.1, 8.2 and 8.3). ΣDDT concentrations ranged from 0.2-9.4 $\mu g/g^{-1}$ lipid weight (mean=1.9±2.2) while ΣPCB ranged from 0.3-3.3 $\mu g\ g^{-1}$ lipid weight (mean=0.9±0.6). ΣHCH concentrations were substantially lower than DDT and PCB concentrations, ranging from below detection levels to 0.3 $\mu g\ g^{-1}$ lipid weight (mean=0.01±0.04). Both β- and δ-HCH isomers were absent from or below detection limits in all samples analysed. Of the DDT isomers and PCB congeners, *p, p'*-DDE and the PCBs 28, 118, 153 and 180 were present in all samples analysed.

8.3.1. Concentrations of pollutants with respect to weight and age

Concentrations of *p, p'*-DDD, *p, p'*-DDE, the PCB congeners 118 and 153 and ΣPCB were found to be significantly negatively related to estimated weight only amongst animals involved in STR2 (*p, p'*-DDD: r^2=0.5, $F_{1,11}$=9.2, *P*=0.01; *p, p'*-DDE: r^2=0.4, $F_{1,11}$=6.2, *P*=0.03; PCB118: r^2=0.7, $F_{1,11}$=23.1, *P*=0.001; PCB153: r^2=0.6, $F_{1,11}$=18.0; *P*=0.002; ΣPCB: r^2=0.6, $F_{1,11}$=16.9, *P*=0.002). Concentrations of all organochlorines were not related to estimated weight when only animals from STR1, all females and females of age group three were included.

Concentrations of the PCB 101 were found to be significantly negatively related to age amongst females in age group three (r^2=0.3, $F_{1,19}$=6.0, *P*=0.03). However, this organochlorine was only present above detectable levels in only one animal and as a result, this relationship cannot be regarded as accurate. In all other whales, concentrations of all HCHs, DDTs and PCBs were not related to age. An analysis of similarity with pairwise tests demonstrated no significant differences in organochlorine concentrations between age groups (Global R: -0.06; Sample statistic: 78.8 %; 5,000 randomisations).

Table 8.1: Mean concentrations ± SD of HCHs in southern Australian sperm whales.

	N	Lipid content (%)	α-HCH	β-HCH	γ-HCH	δ-HCH	ΣHCH
All	37	49.2±17.9	0.003±0.01	ND	0.01±0.04	ND	0.01±0.04
STR1	25	55.3±18.0	0.003±0.01	ND	0.01±0.1	ND	0.01±0.1
STR2	12	36.5±8.6	0.002±0.01	ND	ND	ND	0.002±0.01
All females	32	50.4±18.1	0.003±0.01	ND	0.01±0.1	ND	0.01±0.1
Female age group 1	3	56.8±27.8	ND	ND	ND	ND	ND
Female age group 2	4	49.1±30.2	ND	ND	ND	ND	ND
Female age group 3	21	50.9±16.0	0.003±0.01	ND	0.01±0.1	ND	0.02±0.1
Non-lactating females	16	44.4±14.1	0.01±0.02	ND	ND	ND	0.01±0.02
Lactating females	2	41.8±9.9	ND	ND	ND	ND	ND
All males	5	41.3±15.6	ND	ND	ND	ND	ND
Male age group 1	2	44.6±26.9	ND	ND	ND	ND	ND
Male age group 2	3	42.3±12.1	ND	ND	ND	ND	ND
Range	37	16.2-89.3	ND-0.1	ND	ND-0.3	ND	ND-0.3

All values in ug g^{-1} lipid weight.
ND: not detected

Table 8.2: Mean concentrations ± SD of DDTs in southern Australian sperm whales.

	N	*p, p'*-DDD	*p, p'*-DDE	*p, p'*-DDT	ΣDDT	*p, p'*-DDE/ΣDDT	ΣDDT/ΣPCB
All	37	0.2±0.2	1.0±1.0	0.7±1.2	1.9±2.2	0.6±0.2	2.1±1.8
STR1	25	0.1±0.1	0.7±0.5	0.4±0.6	1.2±1.1	0.7±0.2	1.9±1.6
STR2	12	0.4±0.3	1.6±1.4	1.4±1.9	3.4±3.0	0.5±0.1	2.7±2.1
All females	32	0.2±0.2	0.9±0.7	0.7±1.3	1.7±1.9	0.6±0.2	2.1±1.9
Female age group 1	3	0.3±0.4	1.3±1.4	0.3±0.4	1.9±1.6	0.6±0.2	2.2±1.4
Female Age group 2	4	0.1±0.1	1.1±0.8	0.2±0.2	1.4±0.8	0.7±0.2	1.4±0.5
Female Age group 3	21	0.2±0.2	0.8±0.6	0.9±1.5	1.9±2.2	0.6±0.2	2.4±2.2
Non-lactating females	16	0.2±0.1	0.8±0.5	0.5±0.7	1.5±1.2	0.6±0.2	1.8±1.5
Lactating females	2	0.4±0.3	1.5±0.6	3.6±3.8	5.5±4.7	0.3±0.2	7.0±1.6
All males	5	0.3±0.4	1.8±2.1	1.0±1.1	3.1±3.6	0.7±0.2	2.1±1.0
Male age group 1	2	0.6±0.8	2.8±3.7	1.5±2.1	4.8±6.5	0.8±0.3	1.7±1.7
Male age group 2	2	0.2±0.02	1.2±0.7	0.7±0.1	2.1±0.6	0.6±0.2	2.6±0.4
Range	37	ND-1.1	0.2-5.4	ND-6.3	0.2-9.4	0.2-1.0	0.5-8.1

All values in ug g^{-1} lipid weight.
ND: not detected

Table 8.3: Mean concentrations ± SD of PCBs in southern Australian sperm whales.

	N	PCB28	PCB52	PCB101	PCB118	PCB153	PCB180	ΣPCB
All	37	0.03±0.02	0.1±0.04	0.003±0.02	0.3±0.2	0.3±0.2	0.2±0.1	0.9±0.6
STR1	25	0.03±0.03	0.1±0.03	ND	0.2±0.1	0.2±0.2	0.2±0.1	0.7±0.3
STR2	12	0.04±0.01	0.04±0.04	0.01±0.03	0.4±0.4	0.5±0.3	0.3±0.1	1.3±0.8
All females	32	0.03±0.03	0.1±0.04	0.004±0.02	0.2±0.2	0.3±0.2	0.2±0.1	0.8±0.4
Female Age group 1	3	0.03±0.02	0.1±0.1	ND	0.4±0.5	0.4±0.4	0.2±0.1	1.0±1.1
Female Age group 2	4	0.05±0.05	0.1±0.1	0.02±0.1	0.2±0.1	0.4±0.4	0.3±0.1	1.0±0.6
Female age group 3	21	0.03±0.02	0.04±0.03	0.001±.01	0.2±0.1	0.3±0.1	0.2±.0.1	0.8±0.3
Non-lactating females	16	0.04±0.03	0.1±0.04	0.01±0.02	0.2±0.1	0.3±0.2	0.2±0.1	0.8±0.4
Lactating females	2	0.03±0.01	0.02±0.03	0.02±0.02	0.2±0.2	0.3±0.2	0.2±0.1	0.7±0.5
All males	5	0.04±0.02	0.1±0.03	ND	0.4±0.5	0.4±0.4	0.3±0.2	1.3±1.2
Male age group 1	2	0.04±0.03	0.1±0.1	ND	0.8±0.9	0.7±0.8	0.3±0.3	1.9±2.1
Male age group 2	2	0.04±0.01	0.04±0.03	ND	0.2±0.03	0.3±0.1	0.3±0.2	0.8±0.4
Range	37	0.01-0.1	ND-0.1	ND-0.1	0.1-1.4	0.04-1.2	0.1-0.6	0.3-3.3

All values in ug g^{-1} lipid weight.
ND: not detected.

8.3.2. Concentrations of pollutants with respect to stranding groups

When comparing organochlorine concentrations between the two stranding sites, the age of individuals was found to have no effect ($F_{12,17}$=0.8, P=0.6). Individuals involved in STR2 contained significantly higher concentrations of the DDT isomer *p, p'*-DDE and ΣDDT and the PCB congeners 101, 118, 153, 180 and ΣPCB (Table 8.4). When only females were included, similar differences were observed in PCBs, however *p, p'*-DDE and ΣDDT were not significantly different between the two sites. Although γ-HCH was either absent or below detection limits in all animals involved in STR2, its presence amongst individuals from STR1 was also low: it was only detected in one individual. There were no significant differences in the ratios *p, p'*-DDE/ΣDDT and ΣDDT/ΣPCB between individuals from the two sites.

Discriminant function analysis correctly assigned 89.2 % of all cases on the basis of stranding site. Cross-validation using a jackknife analysis also correctly assigned 89.2 % of all cases to the correct stranding group.

8.3.3. Concentrations of pollutants with respect to sex and reproductive groups

The blubber from male sperm whales differed from females in that no detectable concentrations of HCHs or the PCB 101 were present (Tables 8.1 and 8.3). HCHs were also absent from the two lactating females (Table 8.1). An analysis of similarity with pairwise tests demonstrated no significant differences in organochlorine concentrations between reproductive groups or sexes (Global R: -0.04; Sample statistic: 71.0 %; 5,000 randomisations).

8.3.4. Concentrations of pollutants with respect to blubber lipid content

Wet weight concentrations of organochlorines demonstrated different relationships with blubber lipid content across all groups of animals. The PCB congener 118 and ΣPCB demonstrated a positive relationship with blubber lipid content, while *p, p'*-DDD and *p, p'*-DDE demonstrated a negative relationship with blubber lipid content. Concentrations of *p, p'*-DDD demonstrated a significant negative relationship with blubber lipid content in all animals pooled (r^2=0.1; $F_{1,36}$=4.9; P=0.03). Individuals from STR1 demonstrated significant positive relationships between the PCB 118 (r^2=0.3; $F_{1,24}$=10.3; P=0.004) and ΣPCB (r^2=0.2; $F_{1,24}$=4.8; P=0.04; Figure 8.1) and blubber lipid content and a significant negative relationship with *p, p'*-DDD (r^2=0.2; $F_{1,23}$=6.2; P=0.02; Figure 8.1), while those from STR2 demonstrated a significant negative relationship with *p, p'*-DDE (r^2=0.4; $F_{1,11}$=5.8; P=0.04). Females of age group three demonstrated a significant positive

relationship between PCB 118 (r^2=0.2; $F_{1,28}$=8.2; *P*=0.008) and ΣPCB (r^2=0.1; $F_{1,28}$=4.4; *P*=0.05) and blubber lipid content, while all females pooled demonstrated a significant negative relationship between *p, p'*-DDD and blubber lipid content (r^2=0.1; $F_{1,31}$=4.0; *P*=0.05).

Table 8.4: General Linear Model (with age as a co-variate) results from comparisons of pollutant concentrations between sperm whales from the two stranding sites.

	All (d.f. = 2)		All females (d.f .= 2)		Female age group 3 (d.f. = 2)	
Compound	F-ratio	*P*	F-ratio	*P*	F-ratio	*P*
γHCH	0.4	ns	0.3	ns	0.3	ns
ΣHCH	0.4	ns	0.3	ns	0.3	ns
*p, p'*DDD	1.9	ns	2.5	ns	0.5	ns
*p, p'*DDE	5.0	0.01	1.2	ns	1.0	ns
*p, p'*DDT	1.1	ns	0.9	ns	0.6	ns
ΣDDT	5.3	0.01	3.0	ns	2.0	ns
PCB28	2.2	ns	1.1	ns	0.7	ns
PCB52	0.1	ns	0.1	ns	0.04	ns
PCB101	3.3	0.05	3.7	0.04	3.7	0.04
PCB118	8.1	0.002	7.4	0.003	4.2	0.03
PCB153	6.5	0.005	5.0	0.02	3.7	0.04
PCB180	7.0	0.003	5.0	0.02	4.6	0.02
ΣPCB	8.9	0.001	7.7	0.003	4.9	0.02
*p, p'*DDE/ΣDDT	0.9	ns	1.7	ns	2.9	ns
ΣDDT/ΣPCB	2.6	ns	0.3	ns	0.6	ns

ns: not significant

8.3.5. Stratification of pollutant concentrations

The distribution of pollutant concentrations across the vertical aspect of the blubber layer varied between the groups of pollutants (Tables 8.5 and 8.6). While there were exceptions, the general pattern of distribution for: DDTs was inner strata>outer strata>middle strata and the pattern for PCBs: outer strata>inner strata>middle strata (Figure 8.2). HCHs when present, were only present in the inner most strata of the blubber layer and the PCB congener 101 when present was only present in the outermost blubber stratum. Distributions of most compounds were significantly different between the three strata (Table 8.7). Concentrations of α-HCH, ΣHCH, *p, p'*-DDE, the PCB congener 101 and ΣPCB were not significantly different between the three strata.

Small sample sizes prevented an investigation into potential differences in stratification on the basis of reproductive condition, age or sex.

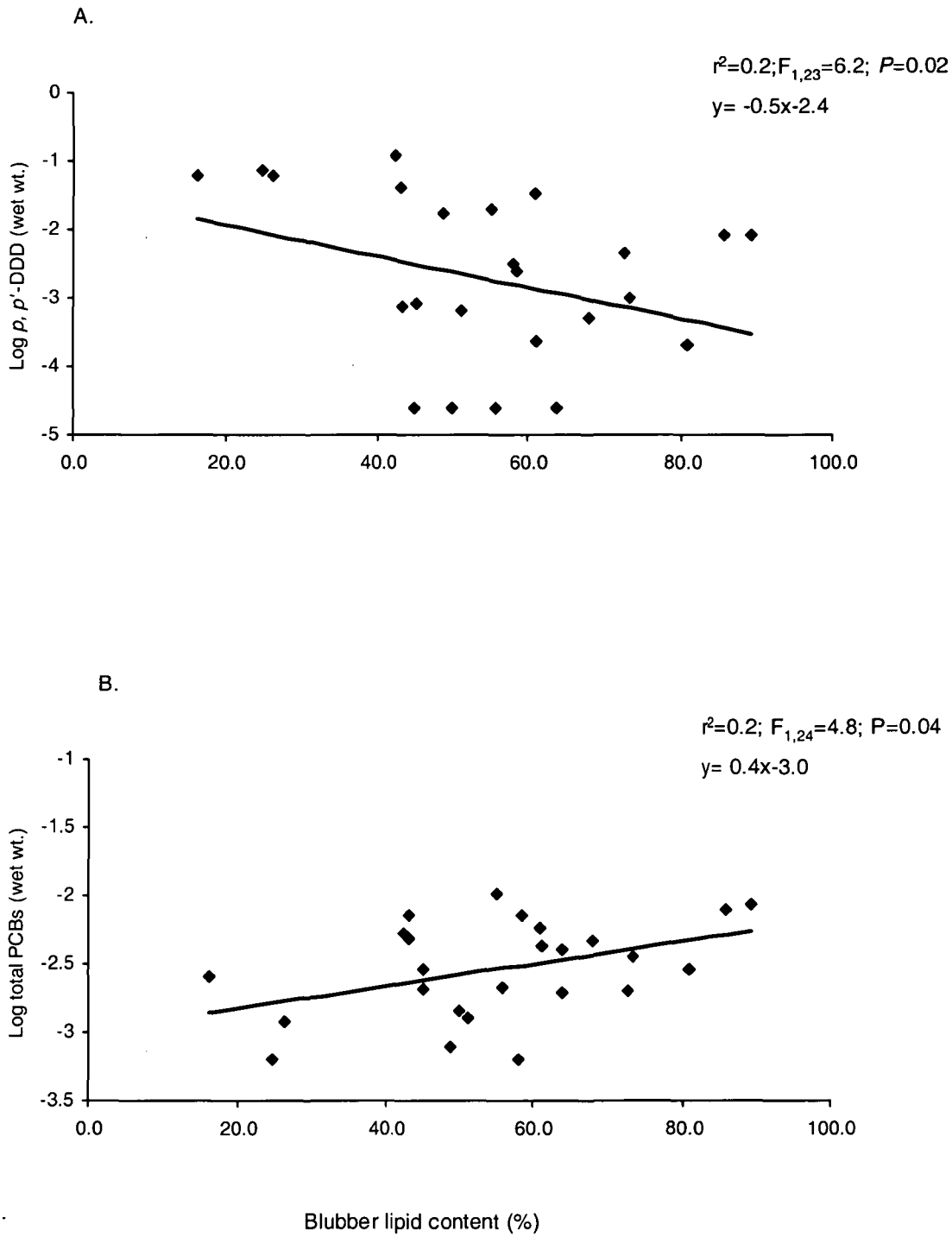


Figure 8.1: Concentrations of (a) *p, p'*-DDD and (b) ΣPCB with blubber lipid content in sperm whales involved in STR1.

8.4. DISCUSSION

The results of this study highlight the complexity of organochlorine accumulation in sperm whales. High variability was associated with concentrations of all organochlorines. Differences between stranding groups support the potential for organochlorines as means of discriminating social and thereby foraging groups of sperm whales, and highlight diet as a primary influence on organochlorine concentrations in this species.

8.4.1. Concentrations of pollutants with respect to weight and age

Typically across marine mammals, both males and females tend to accumulate organic pollutants rapidly during juvenile stages. As males age, accumulation slows and attains a plateau in adults. Females, however demonstrate a sharper slowing in accumulation, with burdens stabilizing and even decreasing in older individuals (Aguilar *et al.* 1999). This difference in accumulation has been attributed to the capacity for lipophillic pollutants to be passed across the placental membrane to the foetus during pregnancy, and through the transfer to dependent young via milk during lactation. Transfer of pollutants to the foetus varies between species and has been reported to be in the order of 5-15 % of the total body burden of the mother (Duinker and Hillibrand 1979; Tanabe *et al.* 1980). Transfer during lactation increases substantially and has been reported to be in the order of 72-98 % of the mother's body burden (Tanabe *et al.* 1980; Cockcroft and Ross 1989). This increase is primarily associated with the depletion of body reserves of fat, protein and minerals to supply precursors for milk synthesis (Pond 1984). The magnitude of organochlorine transfer and therefore overall patterns in lifetime accumulation thereby depends on the reproductive rate of the species and individual, and the intensity of reproductive transfer (Aguilar *et al.*, 1999).

Relationships between pollutant concentrations and age were absent amongst these sperm whales. Large numbers of adult females, a lack of adult males and high individual variation may serve mask any relationships present across the animals in this study. This may be further enhanced by the reproductive history of females in this study. Aguilar and Borrell (1994b) proposed that the highest transfer of pollutants from a mother to calf would occur during a female's first reproductive cycle. With continuing transfer of concentrations during successive reproductive cycles, the overall burden in the female decreases and therefore the amount transferred also decreases. In such a scenario, the first calf from a female would contain the highest pollutant burdens of all of her offspring. The mean age of females sampled was 34.6±14.8 years (0.75-60 years).

Female sperm whales are considered to be sexually mature (but not physically mature) at around ten to13 years, although have been found to be pregnant as early as seven yr (Best *et al.* 1984). Females in this study were, for the majority, older than 20 years (90 %) and therefore are likely to have already given birth to their first calf, thereby offloading the largest portion of their pollutant burdens. Low numbers of juveniles and high individual variation may serve to confound any distinct differences between sexually immature and mature females and further any variation in pollutant burdens within these two groups of females.

Female sperm whales are well known for their gregariousness, forming socially cohesive groups of ten to 30 adult females and immature individuals. These groups are themselves composed of dynamic associations between mostly permanent units of 12 to 13 individuals (Whitehead *et al.* 1991; Richard *et al.* 1996). The complex social structure of sperm whales is fundamentally associated with optimizing the survival of offspring through communal defense and communal care of young (Best 1979; Richard *et al.* 1996). These strategies serve to free lactating mothers from supervisory roles over young, allowing continual foraging and the costs of reproduction to largely be met by feeding thereby minimising demands on energy reserves. A reproductive strategy involving the continuous acquisition of energy throughout the reproductive period, allowing adjustments in energy acquisition in response to changes in energy demands, and a prolonged lactation period, is typical of that of income breeders (Jönsson 1997). The opposite strategy is the reliance on endogenous energy stores during a reproduction period involving fasting and is typical of the reproductive strategies of capital breeders such as baleen whales and a number of phocid species (Jönsson 1997). The reproductive strategy of capital breeders often involves high intensity, relatively short lactation periods involving high energy transfer to young, therefore allowing rapid growth and shorter dependence periods (Oftedal 1997).

Table 8.5: Mean concentrations ± SD of HCHs and DDTs in the outer, middle and inner strata of blubber in southern Australian sperm whales from STR2.

Strata	Group	N	Lipid content (%)	α-HCH	β-HCH	γ-HCH	δ-HCH	Σ-HCH	*p, p'*-DDD	*p, p'*-DDE	*p, p'*-DDT	ΣDDT
Outer	All	10	35.7±14.2	ND	ND	ND	ND	ND	0.3±0.3	1.2±1.2	1.1±2.1	2.6±3.5
	All females	7	35.7±16.2	ND	ND	ND	ND	ND	0.3±0.3	1.2±1.4	1.3±2.5	2.9±4.2
	Non-lactating mature females	5	41.6±14.6	ND	ND	ND	ND	ND	0.2±0.1	0.7±0.2	0.4±0.2	1.2±0.4
	Lactating females	1	28.56	ND	ND	ND	ND	ND	0.2	0.9	0.5	1.61
	Males	3	35.8±10.6	ND	ND	ND	ND	ND	0.2±0.1	1.0±0.5	0.6±0.3	1.8±0.9
	Range		13.2-63.1	ND	ND	ND	ND	ND	0.1-1.1	0.4-4.4	0.1-7.0	0.6-12.4
Middle	All	10	47.7±10.7	ND	ND	ND	ND	ND	0.2±0.1	0.9±0.6	0.7±0.5	1.7±1.2
	All females	7	49.3±12.3	ND	ND	ND	ND	ND	0.1±0.1	0.7±0.4	0.6±0.4	1.4±0.8
	Non-lactating mature females	5	49.6±14.1	ND	ND	ND	ND	ND	0.2±0.1	0.7±0.4	0.5±0.2	1.3±0.6
	Lactating females	1	56.0	ND	ND	ND	ND	ND	0.1	0.3	0.2	0.51
	Males	3	43.9±6.1	ND	ND	ND	ND	ND	0.2±0.2	1.3±1.0	1.0±0.7	2.5±1.8
	Range		28.9-65.5	ND	ND	ND	ND	ND	ND-0.4	0.3-2.4	0.2-1.6	0.5-4.4
Inner	All	10	32.7±13.5	0.01±0.02	ND	ND	ND	0.01±0.02	0.4±0.5	1.4±1.2	2.3±5.6	4.0±7.2
	All females	7	30.6±10.7	0.01±0.03	ND	ND	ND	0.01±0.03	0.4±0.5	1.4±1.4	3.1±6.7	4.9±8.6
	Non-lactating mature females	5	32.5±11.7	0.02±0.04	ND	ND	ND	0.01±0.03	0.2±0.1	0.8±0.4	0.3±0.3	1.3±0.6
	Lactating females	1	19.8	ND	ND	ND	ND	ND	1.6	4.6	18.2	24.3
	Males	3	37.5±15.7	ND	ND	ND	ND	ND	0.1±0.1	1.3±0.8	0.4±0.3	1.8±0.4
	Range		19.8-61.2	ND-0.1	ND	ND	ND	ND-0.1	ND-1.6	0.4-4.6	ND-18.2	0.7-24.3

All values in μg g^{-1} lipid weight.
ND: not detected.

Table 8.6: Mean concentrations ± SD of PCBs in the outer, middle and inner strata of blubber in southern Australian sperm whales from STR2.

Strata	Group	N	PCB 28	PCB52	PCB101	PCB118	PCB153	PCB180	ΣPCB
Outer	All	10	0.1±0.02	0.1±0.1	0.04±0.1	0.4±0.2	0.4±0.2	0.3±0.2	1.3±0.4
	All females	7	0.04±0.01	0.04±0.03	0.1±0.1	0.4±0.2	0.5±0.2	0.3±0.2	1.3±0.4
	Non-lactating mature females	5	0.04±0.01	0.1±0.03	0.1±0.1	0.3±0.2	0.4±0.1	0.3±0.2	1.1±0.4
	Lactating females	1	0.04	ND	0.1	0.5	0.4	0.3	1.4
	Males	3	0.1±0.02	0.1±0.1	ND	0.4±0.2	0.4±0.2	0.4±0.2	1.3±0.5
	Range		0.02-0.1	ND-0.2	ND-0.3	0.2-0.7	0.2-0.9	0.1-0.6	0.7-2.0
Middle	All	10	0.02±0.02	0.02±0.03	ND	0.2±0.1	0.2±0.1	0.3±0.2	0.8±0.4
	All females	7	0.02±0.02	0.02±0.03	ND	0.3±0.1	0.3±0.1	0.3±0.2	0.3±0.2
	Non-lactating mature females	5	0.03±0.02	0.03±0.03	ND	0.3±0.1	0.3±0.1	0.3±0.2	0.9±0.3
	Lactating females	1	0.01	ND	ND	0.2	0.3	0.1	0.7
	Males	3	0.02±0.02	0.01±0.01	ND	0.1±0.1	0.2±0.1	0.2±0.2	0.5±0.4
	Range		ND-0.1	ND-0.1	ND	0.01-0.5	0.01-0.4	0.1-0.7	0.1-1.4
Inner	All	10	0.03±0.03	0.01±0.02	ND	0.3±0.1	0.4±0.7	0.2±0.1	0.9±0.4
	All females	7	0.04±0.03	0.01±0.02	ND	0.3±0.1	0.4±0.2	0.2±0.1	1.0±0.4
	Non-lactating mature females	5	0.04±0.04	0.01±0.02	ND	0.3±0.2	0.5±0.2	0.3±0.1	1.1±0.4
	Lactating females	1	0.04	ND	ND	0.4	0.6	0.3	1.2
	Males	3	0.03±0.01	0.02±0.03	ND	0.2±0.1	0.3±0.1	0.3±0.2	0.8±0.3
	Range		0.01-0.1	ND-0.1	ND	0.1-0.5	0.1-0.7	0.1-0.5	0.4-1.3

All values in $\mu g\ g^{-1}$ lipid weight.
ND: not detected.

Differences in these two reproductive strategies may result in differing patterns of pollutant intake, metabolism and offloading. Offloading of pollutants from income breeding mothers to their young may not become significant until times during which continual foraging cannot meet higher energetic demands associated with lactation and stored energy reserves are therefore required to meet these demands. If body burdens of pollutants are not substantial, fecundity is low and foraging strategies serve to minimize demands placed on energy reserves during reproduction, the overall effect of offloading of pollutants in females may not be obvious. Without detailed information on the reproductive history of individuals, it is difficult to assess the effect of reproduction on the relationships between age and pollutant concentrations observed in this study.

Individuals from STR2 demonstrated a decrease in the concentration of *p, p'*-DDD, *p, p'*-DDE, the PCB congeners 118 and 153 and ΣPCB with estimated weight. This was largely influenced by relatively high concentrations in two immature animals (one female, one male) in this dataset, particularly by a male aged five years, and much lower concentrations in the adult females involved in this stranding. The results observed here therefore may be more associated with age, rather than differences in the size of individuals.

Table 8.7: Results of repeated measures ANOVA on the distribution of pollutant concentrations throughout the blubber layer of southern Australian sperm whales.

Compound	F-ratio (d.f. = 9)	*P*
αHCH	1.0	ns
ΣHCH	1.0	ns
*p, p'*DDD	72.0	<0.001
*p, p'*DDE	1.0	ns
*p, p'*DDT	5.5	0.04
ΣDDT	10.9	0.01
PCB28	318.2	<0.001
PCB52	32.4	<0.001
PCB101	2.0	ns
PCB118	139.3	<0.001
PCB153	76.9	<0.001
PCB180	131.3	<0.001
ΣPCB	2.0	ns

ns: not significant

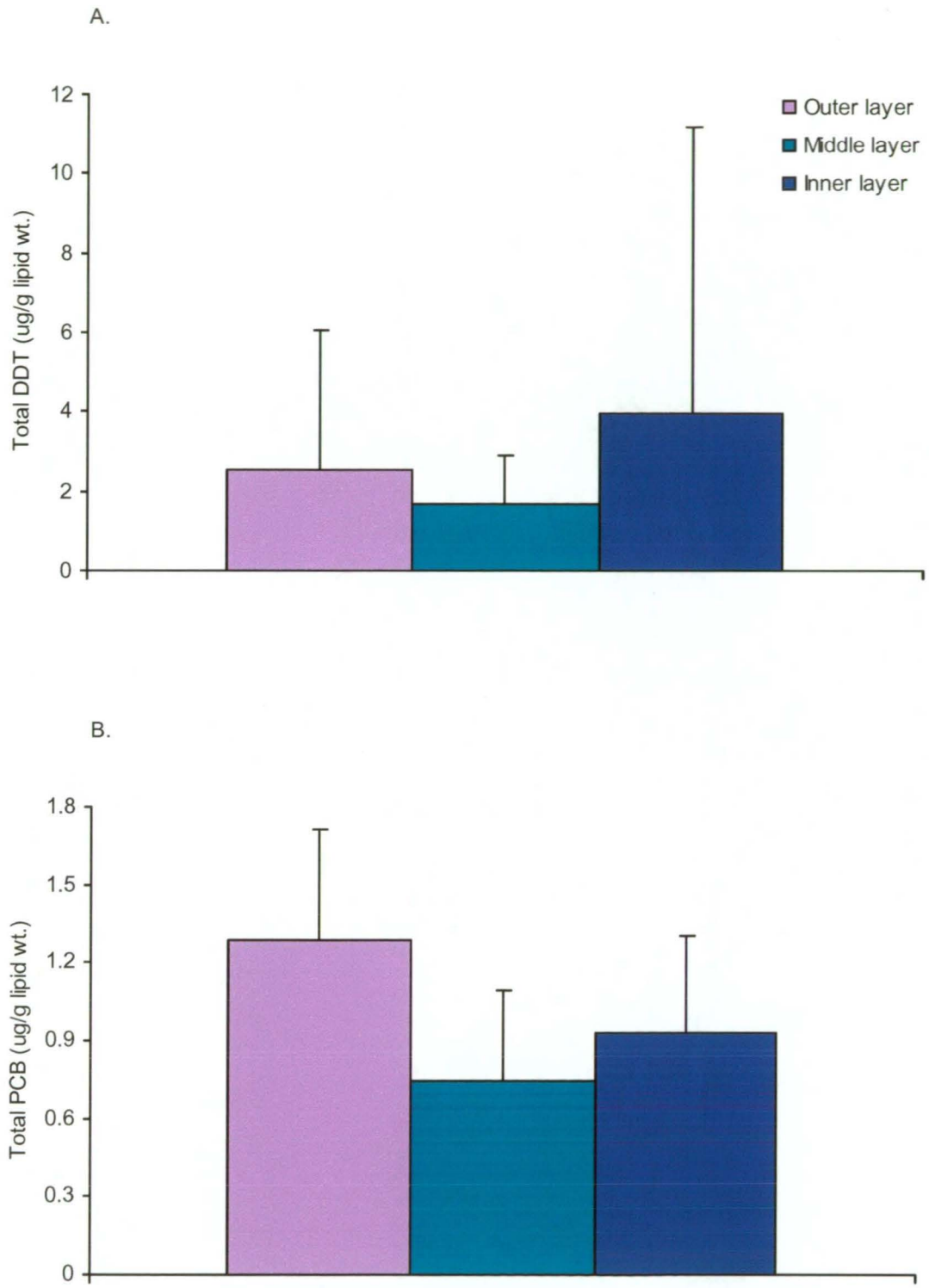


Figure 8.2: Average concentration of (a) ΣDDT and (b) ΣPCB in the outer, middle and inner strata of blubber in southern Australian sperm whales.

8.4.2. Concentrations of pollutants with respect to sex

Males were distinctly different from females in their lack of detectable quantities of HCHs and the PCB 101. This may reflect differences in the intake, metabolism and excretion of individual organochlorines between sexes. However, both pollutants were not common in detectable concentrations throughout all animals in this study: HCHs were only detected in three animals and the PCB 101 detected in two animals. Larger sample sizes are required to establish whether this is indeed an indicator of differential deposition of these organochlorines between males and females. Aguilar (1983) reported higher concentrations of *p, p'*-DDT, *p, p'*-DDE, *p, p'*-DDD, ΣDDT and ΣPCB in female sperm whales but noted that age, reproductive status and fattening condition could mask differences between sexes. Sexual differences in diving ability, migratory habits and diet have been suggested to account for different pollutant inputs and subsequent patterns in pollutant burdens in this species (Aguilar 1983).

While females are largely restricted to waters north of 40°S, males range into higher latitudes, traveling as far as the ice edge. Movements of males into polar, less polluted waters (due to their greater distance from point sources) and the confinement of females to more temperate and tropical and more highly polluted waters (due to their closer proximity to point sources; see Iwata *et al.* (1993) for an overview of global organochlorine distributions) would result in differing inputs and consequently, differing overall burdens between sexes. Differences in the diet of males and females in this area in late summer have been observed (Chapter Six) and may be reflective of different foraging habitats between sexes. However, dietary assessments were marked by high individual variability. This variability, coupled with small sample sizes and a lack of adult males makes it difficult to draw any conclusions on potential differences in organochlorine concentrations between sexes.

8.4.3. Concentrations of pollutants with respect to stranding groups

As most persistent pollutants are incorporated into the bodies of marine mammals via food (Aguilar *et al.*, 1999), differences in the concentrations of organochlorines between the two stranding groups may reflect differences in the composition of diet or in the location of feeding grounds between the two groups. Analysis of the recent diet of individuals revealed differences in the diet between the two stranding groups (Chapter Six), but was characterized by intra-group variation, possibly the result of the presence of discrete foraging units within each stranding group. The nature of the associations between female sperm whale groups has been postulated to be reflective of foraging associations, and the dynamics of these associations vary with prey distributions and densities (Whitehead *et al.* 1991).

Although not statistically significant, differences in the *p, p'*-DDE/ΣDDT (STR1: 0.7±0.2; STR2: 0.5±0.2) and ΣDDT/ΣPCB (STR1: 1.9±1.6; STR2: 2.7±2.1) ratios of the two stranding groups may indicate potential differences in the longer-term diet and movement patterns of the two groups. The ΣDDT/ΣPCB ratio is regarded as one of the most important for use in discriminating different populations of animals because of its sensitivity to distance from land and to trophic level (Aguilar 1984). This ratio is higher in water masses closer to agricultural areas and lower in waters close to industrialised areas. The DDE/ΣDDT ratio is based on the process of conversion of DDT through a chief metabolic pathway via dehydroclorination to its metabolite DDE (Aguilar 1984). This ratio therefore, is dependent on the amount of time since the release of DDT into the ocean and is indicative of differing release chronologies between different areas (Aguilar 1987).

The recent diet of these sperm whales demonstrated that the diet of individuals from the two stranding groups differed and suggests that there may have been some segregation in the foraging of the two stranding groups (Chapter Six). However, these differences were marked by high individual variability and may be influenced by the distribution of males throughout the dataset. Cephalopods distributed throughout tropical and subtropical waters contributed to the diet of individuals from STR1 to a greater extent than they did to the diet of individuals from STR2, while those distributed throughout more southerly waters contributed to a larger extent to the diet of individuals from STR2. If this is a reflection of the longer-term diet of these animals, then individuals from STR1 may have been exposed to more recent inputs of DDT due to closer point source proximity. In the Southern Hemisphere, the vast majority of the populated area is in tropical and

subtropical regions and levels of pollutants in both the air and surface water reflect this distribution (Iwata *et al.* 1993). Assessment of longer-term dietary components through the use of techniques such as fatty acid analysis may provide further insight into the diet of individuals and in association, potential differences in organochlorine accumulation.

The mean blubber lipid content of individuals involved in STR1 (55.3±18.0) was significantly higher than that of individuals involved in STR2 (36.5±8.6; t_{35}=3.32, P=0.002). It is possible that mobilisation of lipids, resulting in lower blubber lipid contents may have also contributed to the observed higher concentrations of pollutant compounds remaining in blubber tissue of individuals involved in STR2.

8.4.4. Concentrations of pollutants with respect to blubber lipid content

Changes to pollutant concentrations as a result of the mobilisation of lipids are thought to involve a combination of two processes: (1) pollutants leave storage sites with the lipids to which they are bound, and pass into the blood and onto to other tissues, or are excreted resulting in tissue concentrations remaining constant; (2) pollutants remain in the tissues (lipids are more readily mobilised than lipophillic compounds), resulting in an increase in concentrations relative to the amount of lipids in the tissue (Aguilar 1987; Aguilar *et al.* 1999). These two processes result in an overall increase in concentrations, but at a lower level than that which a purely concentrative model would produce.

Different organochlorines were observed to demonstrate different relationships between concentrations and blubber lipid content. DDTs decreased with increasing blubber lipid content, following the general pattern of an increase in concentration with mobilisation of lipids (Aguilar *et al.* 1999; see above), while PCBs increased with blubber lipid content amongst individuals from STR1 and in adult females. The relationship between PCB concentrations and blubber lipid content observed in this study is the opposite of that observed in cetaceans elsewhere (Aguilar *et al.* 1999). Although this relationship was statistically significant in adult females and individuals from STR1 (which were dominated by adult females), it was not a strong relationship and may have been biased by small samples sizes and high individual variability (Figure 8.1).

Differences in the behaviour of individual compounds to changes in lipid content may be the result of: (i) differing affinities of individual organochlorines to different lipid groups (ii) differing energetic utilization of lipid groups and (iii) differences in the ability to metabolise specific pollutant compounds. Concentrations of DDTs and highly chlorinated PCBs have been reported to be related to levels of triglycerides and non-esterified fatty acids, while concentrations of less chlorinated PCBs are reported to be

related to levels of the highly polar phospholipids (Aguilar 1985; Kawai *et al.* 1988). Differences in the rate and extent to which these lipids are mobilised would result in differing behaviours of pollutant concentrations associated with those lipids.

Both the diet and blubber lipid content of sperm whales from these strandings was typified by high individual variability (Chapter Six; Chapter Seven), suggesting differences in the feeding intensity and foraging success of individuals. Associated with this, if differing foraging strategies are employed by individuals (*i.e.* differences in the spatial distribution of foraging individuals or differences in dive profiles), this may be reflected in differing metabolic demands on energy stores and therefore, individual variation in the utilization of energy. Both factors would ultimately result in high individual variability in energy stores and subsequently, on concentrations of organochlorines and the exchange in these between the blubber, blood and other organs.

Further studies involving larger number of animals across all age and reproductive groups would serve to establish the relationships of individual organochlorines with lipid content and additionally the effects of gender and individual variation on these relationships.

8.4.5. Stratification of pollutant concentrations

Differential deposition, or mobilisation, of pollutants throughout blubber tissue appears to occur in this species. Stratification of pollutant concentrations throughout the blubber layer has been suggested in fin (*Balaenoptera physalus*) and sei (*Balaenoptera borealis*) whales (Aguilar 1985; Aguilar and Borrell 1990), but has not been documented for this species.

Two interacting factors may contribute to the stratification of pollutant concentrations: (1) lipid composition varies with depth throughout the blubber layer of cetaceans, with inner layers containing longer-chain unsaturated fatty acids and outer layers containing medium-chain fatty acids (Ackman *et al.* 1975a; Koopman *et al.* 1996). Individual organochlorines are reported to demonstrate different affinities for different lipids (Kawai *et al.* 1988; Guitart *et al.* 1996). As a result, the distribution of pollutants may therefore reflect any differential distribution in concentrations of individual lipids throughout the blubber layer. (2) Pollutants are absorbed and released into the blood from organs such as the liver and blubber following changes in the ingestion and excretion rates of compounds (Moriarty 1984). The magnitude of this exchange is dependent on the size of the vascular network supplying each organ. The innermost layer of the blubber is exposed to a much larger circulatory network than the middle and outer layers. As a result, pollutants present in the inner layer of blubber are more easily transferred than

those in the middle and outer layers and consequently, are sites of greater pollutant concentration variability (Aguilar and Borrell 1994b). This exchange may also be enhanced or diminished by the polarity of individual compounds (Aguilar and Borrell 1991).

Investigations into the stratification of pollutant concentrations throughout the blubber layer found that concentrations of DDTs were highest in the inner layer of blubber, while those of ΣPCB were highest in the outer layer of blubber. It must be noted that differences in PCB concentrations between layers were small and not as distinct as those observed in DDT concentrations. Overall concentrations of both DDTs and PCBs were observed to be lowest in the middle layer of blubber of individuals.

Stratification of lipids and constituent fatty acids in harbour porpoises and fin whales suggests that the inner region of the blubber is a more active site for lipid deposition and mobilisation, while the outer layers of blubber are more stable and lipids contained in these layers are not readily mobilized (Ackman *et al.* 1975a; Koopman *et al.* 1996). Preliminary analysis into the stratification of fatty acids in the blubber of sperm whales in this study suggests that constituent fatty acids follow similar patterns to those documented in other species (Bedard 1998). If the majority of lipid deposition occurs in the inner layers of blubber and the outer layers are relatively stable sites, pollutants stored in the outer layers of the blubber may not necessarily undertake the same patterns in concentration changes demonstrated by those pollutants stored in the inner layers of the blubber. If lipids are not readily mobilized from the outer layers of blubber and PCBs concentrate in these areas due to constituent lipid preferences, the outer layers of blubber may ultimately serve as pollutant reservoirs, concentrating PCBs. Further studies into the distribution of organochlorines throughout the blubber layer are required to ascertain whether greater concentrations of PCBs accumulate in the outer layer of blubber and that therefore, DDTs and PCBs are distributed differently throughout the blubber layer in sperm whales.

The presence of stratification in organochlorine concentrations suggests that no single section of the blubber layer of sperm whales is necessarily more representative of overall pollutant concentrations in this organ. This must be considered when comparing concentrations of pollutants between animals from different studies, particularly those based on samples from live whales obtained with the use of biopsy darts. These sampling methods do not penetrate the whole blubber depth in large whales such as sperm whales, taking only a fraction of the outer blubber layer, and therefore, may not provide a

comprehensive indication of the presence and concentration of pollutants in blubber tissue. Comparisons from or with such studies must be undertaken with care, in light of possible biases due to stratification.

8.4.6. Concentrations of pollutants with respect to sperm whales elsewhere

The overall mean concentrations of organochlorines were relatively low compared to those documented in this species in the Northern Hemisphere (Table 8.7). However, some individuals demonstrated concentrations of organochlorines comparable to, or above levels found in a number of studies of sperm whales in the Northern Hemisphere. Mean concentrations of compounds were comparable or higher than those previously reported for this species in the Southern Hemisphere. Differences in analytical techniques, lack of gender specification, biases to adult males and presentation of results without relation to lipid amounts confound comparisons. It has been well established that differences in analytical techniques, the presentation of results and differences in the life history and biology (*e.g.* size, sex, age, diet, nutritive condition, health) of individuals can have significant effects on the ability to make inter-study comparisons (Aguilar *et al.* 1999). Additionally, as observed in this study, different groups of sperm whales from the same region can demonstrate differences in organochlorine concentrations. Differences in the dietary composition and foraging areas of groups are likely to result in differing intakes of organochlorines and as a result, it is difficult to positively identify temporal changes in organochlorine concentrations across large regions.

The highest concentrations of organochlorines in sperm whales were those of DDT and its metabolites, while concentrations of PCBs were considerably lower. This is also been observed in the majority of sperm whales studied elsewhere (Table 8.7). Concentrations of PCBs exceeded those of DDTs only in animals from the eastern North Atlantic and around Iceland (Aguilar 1983; Borrell 1993). This may be a reflection of global pollutant inputs, atmospheric and oceanic transport of pollutants and the metabolic capabilities of this species. Striped and bottlenose dolphins and fin whales have also been reported to have higher body loads of DDTs than PCBs. Subsequently, it has been hypothesized that DDT compounds are less easily metabolized than PCBs in cetaceans (Aguilar and Borrell 1994b). Of the concentrations of individual PCB congeners, individuals in this study contained higher concentrations of the congener 153. This congener is highly bio-persistent (Van den Berg *et al.* 1998) and a similar dominance of this congener in PCB concentrations has been reported in a number of other cetacean species including sperm whales (Law *et al.* 1996; Holsbeek *et al.* 1999; Minh *et al.* 2000). The position of and degree of halogenation in PCBs and species-specific differences in the reaction of metabolic enzyme systems to these pollutants determine the rate and degree of

metabolism of PCBs. This therefore determines the excretion or bioaccumulation of these compounds (Van den Berg *et al.* 1998). Preferential metabolism and elimination of PCBs has been inferred in a number of cetacean species from occurrence patterns in pollutants between predators and their prey, and the reactions of enzyme systems associated with the metabolism of toxic compounds such as the cytochrome P450 1A enzyme system (Kannan *et al.* 1989; Tanabe *et al.* 1988; Ross *et al.* 2000). It is possible that this also occurs in sperm whales. Further research investigating the enzyme systems responsible for the metabolism of organochlorines, such as the cytochrome P450 family would provide greater insight into congener specific metabolism in this species.

DDT and PCB concentrations in southern Australian sperm whales were on the whole, less than those reported to be linked with deleterious effects in other marine mammal species (Béland *et al.* 1993; Ross *et al.* 1996; Subramanian *et al.* 1997; Jepson *et al.* 1999). However, the intake, metabolism, excretion and physiological reaction to pollutant concentrations are species-specific (Reijnders 1994) and as a result, it is difficult to extrapolate the effects observed in one species to concentrations of organochlorines in another species. Additionally, a number of organochlorines are reported to undergo multiple non-additive interactions producing responses in mammalian systems at lower concentrations than if introduced individually (*e.g.* synergistic interactions between PCBs and dioxins in the development of porphyria and induction of cytochrome P450 enzyme systems and thyroid hormone levels in rodents) (Van den Berg *et al.* 1998). *In vitro* studies on sperm whale tissues could serve to provide some indication of the effects of changes in concentrations of individual organochlorines and any interactive effects in organ systems.

Continued monitoring of concentrations of organochlorines in oceanic species is essential in establishing temporal trends in regional organochlorine concentrations in cetaceans in the Southern Ocean. This can only be realised through the co-ordinated execution of a program in which associated life history, distribution and migratory data (to account for local and regional pollution influences) are collected. This information, linked with toxicokinetic studies, will provide a better understanding of the effects of such concentrations both in the short and long-term on populations of cetaceans in this area.

Table 8.8: Mean concentrations ± SD (range) of organochlorines in sperm whales elsewhere.

Location	Year	Sex	n	DDT	DDE	DDD	ΣDDT	ΣPCB	ΣHCH	γ-HCH	*p, p'*-DDE/ ΣDDT	ΣDDT/ ΣPCB
South Africa[1]	1974	F	1	ND	0.4	ND	0.4	ND	–	–	1.0	–
		M	11	0.4±0.4 (ND-1.3)	0.4±0.1 (0.2-0.7)	0.01±0.02 (ND-0.1)	0.8±0.5 (0.3-1.9)	ND	–	–	0.6±0.2 (0.4-1.0)	–
South Africa[2*]	1976-81	F	1	0.1	0.1	0.04	0.13	ND	–	–	0.7	–
		M	1	ND	0.2	ND	0.2	ND	–	ND	1.0	–
South Africa[3^]	1978	U	1	–	–	–	1.0	–	–	–	–	–
South Africa[4*]	1986	F#	1	–	–	–	0.4	0.1	–	–	–	3.0
Australia[5*]	U	U	1	–	–	–	8.6	0.2	0.2	–	–	53.8
Australia[6^]	U	U	1	0.6	0.1	0.6	1.2	–	–	–	0.1	–
		F	1	0.2	0.1	0.5	0.8	–	–	–	0.1	–
California[7]	1968	F	4	0.01±0.01 (0.0-0.02)	3.8±0.5 (3.3-4.4)	0.5±0.1 (0.5-0.6)	4.3±0.6 (3.8-5.0)	–	–	–	–	–
		M	2	1.7±1.2 (0.9, 2.6)	3.4±3.7 (0.7, 6.0)	0.5±0.4 (0.2, 0.8)	5.6±5.4 (1.8, 9.4)	–	–	–	–	–
West Indies[8*]	1971-75	F	1	4.0	9.9	1.6	15.5	4.0	–	–	0.6	3.9
		M	1	0.2	0.8	0.1	1.1	0.7	–	–	0.7	1.6
Massachusetts[8*]	1971-75	F	1	3.7	4.6	0.6	8.9	2.1	–	–	0.5	4.2
Eastern North Atlantic[9]	1979-80	F	6	2.7	4.0	0.5	7.7	15.6	–	–	–	–
		M	8	1.2	2.9	0.5	5.1	9.9	–	–	–	–
Iceland[10]	1982	M	10	2.5±1.1	4.2±1.0	1.1±0.2	7.8±1.5	10.5±2.1	–	–	0.5±0.1	0.8±0.1
Orkney Islands[11]	1994	M	3	3.3±0.9 (2.3-3.4)	7.1±1.9 (5.3-9.1)	0.8±0.2 (0.5-0.9)	11.2±2.9 (8.1-13.9)	3.5±1.0 (2.4-4.4)	0.1±0.02 (0.1-0.14)	0.1±0.02 (0.07-0.1)	0.6±0.03 (0.61-0.66)	3.2±0.2 (3.0-3.4)
Wadden Sea[11]	1994	M	1	3.7	5.3	0.7	9.7	3.9	0.2	0.2	0.6	2.5

Table 8.8 continued

Location	Year	Sex	n	DDT	DDE	DDD	ΣDDT	ΣPCB	ΣHCH	γ-HCH	*p, p'*-DDE/ ΣDDT	ΣDDT/ ΣPCB
Netherlands[11]	1995	M	3	4.8±1.0 (3.6-5.5)	8.3±1.7 (6.4-9.7)	1.2±0.3 (0.9-1.4)	14.3±3.0 (10.9-16.5)	4.8±1.2 (3.5-5.7)	0.2±0.01 (0.2-0.2)	0.2±0.01 (0.18-0.19)	0.6±0.01 (0.58-0.59)	3.0±0.1 (2.9-3.2)
Orkney Islands[12+]	1994	M	11	–	–	–	2.7 (1.2-15.5)	1.1 (0.3-6.3)	–	–	–	–
Scotland[12+]	1993-95	M	3	–	–	–	11.5 (11.4-11.6)	5.3 (3.9-5.6)	–	–	–	–
Belgium[12+]	1994	M	4	–	–	–	6.9 (5.3-12.7)	4.6 (3.0-16.4)	–	–	–	–
Netherlands[12]	1995	M	3	–	–	–	–	4.8 (2.8-4.9)	–	–	–	–
Belgium[13]	1994	M	4	3.1±0.4 (2.7-3.5)	4.0±0.7 (3.0-4.6)	0.7±0.04 (0.6-0.7)	7.7±1.1 (6.4-8.9)	2.9±0.3 (2.5-3.2)	0.03±0.01 (0.02-0.03)	–	0.5±0.03 (0.47-0.54)	2.7±0.4 (2.2-3.1)
Netherlands[13]	1995	M	3	2.6±1.0 (1.6-3.6)	4.4±1.4 (2.9-5.7)	0.8±0.2 (0.5-1.0)	7.8±2.6 (5.0-10.3)	3.2±1.0 (2.1-4.2)	0.02±0.01 (0.02-0.03)	–	0.6±0.02 (0.55-0.58)	2.4±0.03 (2.4-2.5)

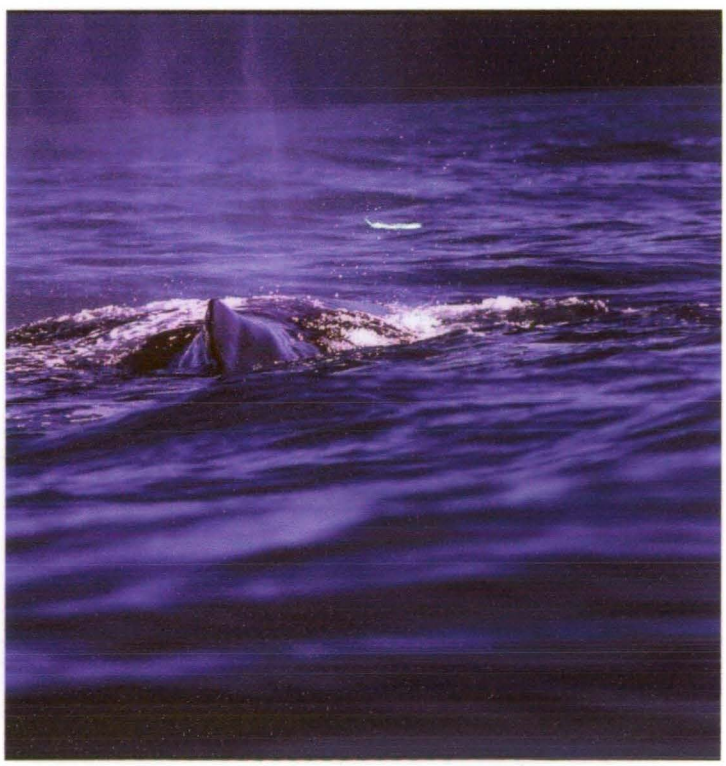
All concentrations μg g^{-1} lipid weight except * μg g^{-1} wet weight and ^ where not stated.
+median instead of mean given.
F: female; M: male; U: not stated.
#uncertainty to identification of sex as total length stated as 16.0m.
[1]Henry and Best (1983). ΣDDT derived from *p, p'* isomers of DDTs, ΣPCB quantified from 4 major peaks in Aroclor 1254 (congeners not identified); [2]Cockcroft and Ross (1991). Does not state whether DDTs *p, p'* or *o, p'* isomers or how ΣDDT and ΣPCB were quantified; [3]Van Dyk *et al.* (1982). Does not state how ΣDDT was quantified; [4]de Kock *et al.* (1994). Does not state how ΣDDT was quantified. ΣPCB was derived from the identification of congeners from standard congener mixtures (all congeners not identified); [5]Kemper *et al.* (1994). Does not state whether DDTs *p, p'* or *o, p'* isomers or how ΣDDT and ΣPCB were quantified; [6]Anderson (1991). Does not state whether DDTs *p, p'* or *o, p'* isomers or how ΣDDT and ΣPCB were quantified; [7]Wolman and Wilson (1970). ΣDDT derived from *o, p'* and *p, p'* isomers of DDTs; [8]Taruski *et al.* (1975). Does not state whether DDTs *p, p'* or *o, p'* isomers or how ΣDDT was quantified. ΣPCB was derived from the sum of the heights of those peaks in the sample that matched Aroclor 1254 and 1260 (congeners not identified); [9]Aguilar (1983). DDTs shown are *p, p'* isomers. ΣDDT derived from the sum of both *p, p'* and *o, p'* isomers. ΣPCB was derived from the sum of the heights of those peaks in the sample that matched Aroclor 1254 and 1260 (congeners not identified); [10]Borrell (1993). DDTs shown are *p, p'* isomers. ΣPCB was derived from the sum of the heights of those peaks in the sample that matched Aroclor 1254 and 1260 (congeners not identified); [11]Law *et al.* (1996). DDTs shown are *p, p'* isomers. ΣDDT derived from the sum of both *p, p'* and *o, p'* isomers. ΣPCB was derived from the sum of the ICES7 congeners; [12]Wells *et al.* (1997). ΣDDT derived from the sum of both *p, p'* and *o, p'* isomers. ΣPCB was derived from the sum of the ICES7 congeners; [13]Holsbeek *et al.* (1999). ΣDDT derived from the sum of both *p, p'* and *o, p'* isomers. ΣPCB was derived from the sum of the ICES7 congeners.

8.5. SUMMARY

- Concentrations of *p, p'*-DDT, *p, p'*-DDE, *p, p'*-DDD, α-HCH, β-HCH, γ-HCH and the PCB congeners 28, 52, 101, 118, 153 and 180 were measured in sperm whales involved in two mass stranding events (STR1 and STR2) on the west coast of Tasmania, Australia in February 1998
- Concentrations of HCHs were low, occurring in detectable concentrations in only three individuals. DDTs and PCBs were present in all samples analysed.
- Only individuals from STR2 demonstrated a relationship between organochlorine concentrations and estimated weight in individuals. No relationships between organochlorine concentrations and age were observed in either group. Detectable concentrations of HCHs and the PCB 101 were not present in the blubber of males.
- Differing individual dietary intake of organochlorines, changes in concentrations associated with the mobilisation of lipids, and individual variation in the ability to metabolise and excrete organochlorines are probable factors affecting the concentrations of organochlorines in sperm whales observed here.
- Concentrations of all pollutants were stratified throughout the vertical aspect of the blubber. The distribution of contaminants throughout the blubber layer may be the result of the dynamics of blubber lipid mobilisation, the differing affinities individual compounds have for various lipids and differing intensities of exchange throughout the blubber to the blood.
- Overall concentrations of compounds were relatively low in comparison to those documented in sperm whales in the Northern Hemisphere, however concentrations were higher than those documented in this species in the Southern Hemisphere previously, although it is difficult to separate spatial and temporal differences from differences associated with analytical techniques and presentation of data.

SECTION FIVE

GENERAL DISCUSSION



CHAPTER NINE

GENERAL DISCUSSION

9.1. THE STUDY

The life history of sperm whales in the Australian region is poorly understood. This paucity of knowledge is reflected in the classification of this species as "insufficiently known" in the Australian Government's recent Action Plan for Cetaceans (Bannister *et al.* 1996). This is despite a lengthy focus of the whaling industry on this species in this region and the extensive analysis of samples and data from whaling catches (Bannister 1969; 1974; 1977; Kirkwood and Bannister 1980; Kirkwood *et al.* 1980). Given the entirely pelagic life cycle of this species and the lack of information on the distribution, seasonality, residence and number of sperm whales in this region, studies on live animals pose many difficulties. As a result, comprehensive studies on live populations of this species in the Australian region have not been logistically or financially feasible. Stranded, dead animals can however, provide a wealth of information both in the short and long term.

Mass strandings of sperm whales in Tasmania are an infrequent, but regular event, occurring approximately every five to ten years and present valuable opportunities to obtain information on this species in the Australian region. The mass stranding of three complete or near-complete female groups of sperm whales along the Tasmanian coastline in 1998 therefore, provided a unique opportunity to study the life history of this species in the southern Australian region.

The aims of this project were:

1. To determine the demographic characteristics of the three groups by:
    - identifying the age structure of the three groups using refinements to contemporary age determination techniques;
    - calculating life table parameters, including survival for mature females;
    - describing growth in females using established growth models.

2. To determine components of energy acquisition and the relationship between energy storage and life history strategies of this species by:
    - quantifying diet composition using hard part identification methods and interpreting differences between sex, age and stranding groups;
    - quantifying body fat condition via blubber thickness measurements and an analysis of blubber lipid content and interpreting these in light of mechanisms of energy storage and mobilisation.

3. To ascertain baseline data on organochlorine levels in this species and provide an ecological interpretation of concentrations and their distribution by:
    - quantifying concentrations of organochlorines from blubber samples;
    - interpreting those concentrations in light of dietary, blubber lipid content and demographic data;
    - interpreting these data in light of what is known for other marine mammals in the Southern Hemisphere.

This project was based on samples collected from the mass-strandings of sperm whales at Ocean Beach, Strahan (STR1), Greens Point Beach, Marrawah (STR2) and Black River Beach, Stanley (STR3). Detailed discussions of the findings from each of these objectives have been presented in Chapters Two to Nine. This chapter will synthesize those findings and present an integrated account of the life history of female groups of sperm whales in southern Australian waters.

9.2. SUMMARY

The broad objective of this project was to investigate the life history of complete or near complete female groups of sperm whales in an effort to further our knowledge of this species in the Australian region. This study has resulted in a series of largely independent chapters which, when considered together, reveal a life history characterised by high individual variability both on a inter-group and intra-group basis, facilitated by a complex social system. The low fecundity of female sperm whales requires the continued survival of offspring to be of paramount importance and the foraging strategies, high sociality, reproductive strategies and life history traits of this species all reflect this. Individual variation, particularly in energy acquisition as observed in this study, can be observed to have flow-on effects for other components of the life history of this species such as energy storage and pollutant burdens.

Often only part of a group of animals can be sampled from or collected at the one time due to the behaviour of these groups at sea, or because of logistical restrictions at mass stranding events. This study presents samples and data collected from complete or near-complete groups of female sperm whales. The majority of current life history information on sperm whales has been derived from whaling catches and is therefore, only representative of exploited populations and that component of the population hunted (*i.e.* large adults). This study presents samples and data collected from a largely unexploited population (some females in this study based on ages determined would have been alive during commercial exploitation which ended in Australian waters in 1978), information which is essential in understanding the life history of this species unbiased by exploitation and in understanding the effects of exploitation on sperm whale populations.

9.2.1 Demography of female sperm whales

Due to the inability to verify age estimates in this species and the subjectivity of the interpretation of dentinal growth layer groups by individual readers, methods by which greater standardization of age estimates could be attained were developed by this study. Modifications of current preparation techniques based on the size and density of individual teeth were found to produce clear, discernible dentinal growth layers groups, without potential over-etching of surfaces. Use of photographic methods, producing greater contrast between growth layer groups and therefore increasing precision of age estimates is encouraged, as their utilization is also a means by which age estimates can be verified by other readers, ensuring interpretation of the same structures and confidence in comparing GLG counts produced in different studies. These issues are of particular

concern when calculating age-specific parameters for use in comparative studies.

While age estimates in this study were found to have a high degree of precision, the effects of tooth wear (which was present on all teeth from individuals older than 20 years) and occlusion events (mineralisation interferences) on the accuracy of age estimates is largely unknown. This has implications for age-specific population parameters. In order to account for the effects of changes on the age structure due to underestimation of age estimates on population parameters, we modeled a scenario involving random, differential tooth wear and occlusion events on the group. Based on the comparison of 100 randomisations, we felt that the median of these Monte Carlo simulations was likely to be a closer representation to the age structure of this group of sperm whales without the effects of tooth wear and occlusion events.

Female sperm whales, unlike many other mammals, demonstrate high, relatively stable survival throughout their entire life span (mean=0.921±0.045; range: 0.866-0.991). The greatest decrease in survival appears to occur in mature females between the ages of 25 to 50 years (a decrease from 0.976 to 0.876). Similar changes in the survival of females have also been recorded in sperm whales elsewhere, with mortality increasing from the ages of 20 to 27 years in female sperm whales from South African whaling fisheries (Best, 1970). Long-finned pilot whales and orcas also demonstrate a decrease in survival between the ages of 30 and 40 years from previous relatively stable rates of survival during the adult stage (Olesiuk *et al.* 1990; Bloch *et al.*, 1993; Brault and Caswell, 1993). The stage at which this escalated decrease in survival occurs may be typical of the longevity of these species.

Overall, growth is prolonged in female sperm whales, not reaching an asymptotic length until around 20 years. Longevity, low fecundity, slow growth, delayed sexual maturation, prolonged parental care, and a low finite rate of increase define sperm whales as extreme K-selected animals (Boyce 1984). Social complexity appears to be one evolutionary strategy enabling high overall survival and is typical of a number of other extreme K-selected species such as long-finned pilot whales (*Globicephala melas*), orcas (*Orcinus orca*), African elephants (*Loxodonta africana*) and humans (*Homo sapiens*).

The higher survival rates observed in the Australian populations in comparison with those from Japanese waters could be the result of either (i) higher rates of exploitation on mature female sperm whales in Japanese waters; (ii) differing natural mortality rates between the two populations or (iii) mis-representation of the age structure of mature female sperm whales caught in Japanese whaling catches. The lack of difference between overall mean survival rates observed in female sperm whales from Western Australian whaling fisheries suggests that there has been little change in the survival rate of mature females post-whaling. However, there appear to have been some changes in the age structure of female sperm whale groups with increases in the average age of individuals and additionally increases in the average total lengths of individuals, which indicate some post-whaling demographic changes.

9.2.2. Energy acquisition and storage in sperm whales

Sperm whales are predators of mesopelagic oceanic waters, a characteristic shared by all populations studied to date. Subtropical and sub-Antarctic species of cephalopods dominated the diet of southern Australian sperm whales, but a high level of both inter- and intra-group variability in the diet was apparent. Dominant cephalopod prey species were similar to that of sperm whales elsewhere in the Southern Hemisphere and included members of the Histioteuthidae, Ommastrephidae, Onychoteuthidae, Architeuthidae, Cranchiidae and Pholidoteuthidae families. While smaller species (<300 mm dorsal mantle length) were numerically abundant, larger species (> 1,000 gm) were clearly important to sperm whales (comprising 78.6 % of the total estimated wet mass) and are likely to provide an efficient means of acquiring energy for this species.

The extensive distribution of sperm whales as a species is facilitated by the ability to undertake foraging movements across large spatial scales and efficiently utilise such a diverse and abundant prey group as the Cephalopoda. An ability to range across large distances and to attain great depths allows movement from low density prey areas to those of higher prey density. This, in turn, facilitates continued foraging success in light of oceanic variability and associated changes in prey abundance. Continuous acquisition of foodenables the ability to meet increased energetic demands associated with reproduction without specific reliance on reserved energy stores.

Two of the stranding groups STR1 and STR2, appeared to be composed of a number of foraging groups, possibly reflecting both individuals and social units that had merged to form larger foraging groups prior to the strandings. These foraging groups of sperm whales may have been segregated by age and gender, although it is difficult to separate

the two effects. High intra group variability in the diet is likely to be associated with separation of foraging individuals at depth (Watkins and Schevill 1977) and may be a reflection of flexibility in the foraging strategies employed by individuals.

Individual variability in foraging success and therefore, in the acquisition of energy will be reflected in an individuals energy stores. High individual variability characterised both blubber thickness and blubber lipid content in southern Australian sperm whales and suggests that deposition (acquisition) and mobilisation (utilization) of energy stores differed between individuals.

Blubber thickness and lipid content may be largely independent of each other in sperm whales and this may be due to the broader role of blubber in sperm whales, the mechanisms of lipid mobilisation from the blubber and the life history of this species. Social groups of female sperm whales providing communal defense and care of young to others within that group would serve to free lactating mothers from supervisory roles over their young. This would allow a lactating mother to continually forage, reducing the need to draw on energy reserves to meet energetic demands associated with lactation. Blubber lipid content would thereby be highly variable within a group, reflecting individual variation in energy acquisition and utilisation.

Stratification of blubber lipid content has been associated with the differential deposition and mobilisation of lipids associated with energy acquisition and metabolism (Koopman *et al.* 1996) and with structural demands associated with thermal regulation (Fredheim *et al.* 1995). Observations of blubber lipid stratification suggest the inner layer is more metabolically active and the outer layer has a more structural role than other layers. However, it is unclear to what extent the differential energetic budgets of capital (some phocids, fin whales) and income breeders [sperm whales; harbour porpoises appear to exhibit a life history somewhere between the two (Read 1990b; Read and Hohn 1995)] may have on the deposition and mobilisation of lipids and their subsequent stratification within the blubber layer.

9.2.3. Influences of the life history of sperm whales on organochlorine concentrations

Organochlorines were present in the blubber of all sperm whales sampled in this study. The relationships between organochlorines, sexes, age and reproductive groups were marked by high individual variability and highlight the complexity of organochlorine accumulation in this species. Differences in analytical techniques, the presentation of results and differences in the life history and biology (*e.g.* size, sex, age, diet, nutritive condition, health) of individuals can have significant effects on the ability to make inter-study comparisons. Additionally, as observed in this study, different groups of sperm whales from the same region can demonstrate differences in organochlorine concentrations. Differences in the dietary composition and foraging areas of groups are likely to result in differing intakes of organochlorines and, as a result, it is difficult to positively identify temporal changes in organochlorine concentrations across large regions. Organochlorine concentrations were on the whole lower than those observed to be linked with deleterious effects, however, it is difficult to draw clear conclusions from this due to species-specific intakes, metabolism, and physiological reactions to pollutant concentrations.

Low fecundity, minimizing the potential for females to offload pollutants to their young and an income breeding reproductive strategy may further serve to confound gender based and age differences in pollutant concentrations. Offloading of pollutants from income breeding mothers to their young may not become significant until times during which continual foraging cannot meet higher energetic demands associated with lactation and stored energy reserves are therefore required to meet these demands. If body burdens of pollutants are not substantial, fecundity is low and foraging strategies serve to minimize demands placed on energy reserves during reproduction, the overall effect of offloading of pollutants in females may not be significant.

The influence of the mobilisation of lipids was also reflected in the stratification of organochlorine concentrations throughout the blubber layer. The stratification of organochlorine concentrations and differing relationships of DDTs and PCBs with blubber lipid content may be a reflection of three factors: (i) differing affinities of organochlorines to different lipid classes; (ii) differing energetic utilization of lipid classes and (iii) differences in the ability to metabolise different pollutant compounds.

9.3 SOCIALITY AND LIFE HISTORY

9.3.1. The evolution of life history traits

The evolution of life history traits and their flexibility determine the population dynamics of a species (Stearns 1992). Life history theory is based on two complimentary components: (i) phenotypic condition, which is concerned with variation in the 'fitness' [the composite of all life history traits associated with the survival of an individual or population (Roff 1992; Stearns 1992)] of individuals and (ii) genotypic condition, which is concerned with the consequences changes in fitness have for gene frequencies (Stearns 1992). The variability associated with life history strategies is tied closely with the availability of resources to a species, the population density and the demography of that species.

Life history traits centre around reproduction and survival and involve a trade-off between the energetic costs of growth, maintenance and reproduction (Roff 1992; Boness *et al.* 2002). The age of sexual maturation and survival of an individual are key factors in the life history strategy of a species and changes in these have large influences on fitness (Stearns 1992). Delaying sexual maturation places larger emphasis on successful reproduction and survival later in life and as a result, mammal species that delay sexual maturity tend to be large, long-lived and have few, well-developed offspring per breeding cycle (Harvey and Read 1985; Stearns 1992; Boness *et al.* 2002). Survival of those few offspring is imperative and subsequently, maternal inputs of energy and time per offspring are high. Methods of energy acquisition and the amount of energy acquired are therefore central links between physiological ecology, behavioural ecology and life history evolution (Stearns 1992).

9.3.2. The life history of female sperm whale in southern Australian waters

Adult female and immature sperm whales of both sexes live in fission-fusion societies of mixed matrilines and long-term associations (Mesnick *et al.* 2003) based on groups of ten to 30 individuals that move and act together in a coordinated manner (Best 1979; Whitehead *et al.* 1991). These groups are themselves composed of mostly permanent units of 12 to 13 individuals (Whitehead *et al.* 1991, Richard *et al.* 1996; Christal and Whitehead 2001). Associations between these units are fluid and have been postulated to be related to foraging, with the dynamics of these associations varying with prey distributions and densities (Whitehead *et al.* 1991). Preliminary genetic studies of these three female groups of sperm whales support the presence of both 'kith' (close, but not

genetically related companions) and 'kin' in these groups (Mesnick *et al.* 2003). These results suggest that individuals from each of the stranding groups were observed to comprise both close relatives and individuals that were not closely related to others (*e.g.* Figure 9.1).

The social groups of female sperm whales are the foundation for the ecological success of sperm whales and have co-evolved with other life history traits to ensure the high life-time survival such as that observed in this study. Yet despite the high dependence on life as a social "unit", this study highlighted the influence of individuality on the life history of female sperm whales. Indeed, it may be that the sociality of this species allows such individuality to influence many parts of a sperm whales life history.

The catholic diet of sperm whales on a highly abundant, widely distributed prey group such as the Cephalopoda and the ability of sperm whales to range across large distances and attain mesopelagic depths, serve to increase foraging success by allowing flexibility in foraging strategies. Changes in prey density can be met by movement to more optimal foraging areas. Changes in the vertical distribution of prey can be accounted for by associated changes in depths attained during diving. Variation in hunting strategies employed enables both muscular fast swimming prey species and gelatinous slow swimming species to be attained.

Segregation of individuals whilst foraging coupled with continual communication, as observed in other studies (Watkins and Schevill 1977; Watkins *et al.* 1993), allows an animal to act as individual whilst still part of a group functioning as a foraging unit and therefore maximizes the efficiency of prey aquisition. Areas containing low prey abundance are not repeatedly searched and areas of high prey abundance are identified to others rapidly. Searching efficiency for sparce and patchy prey aggregations is maximized. Prey resources utilized will as a result, be a combination of those identified by the individual (in the case of small patches of prey) and those identified by the foraging group (in the case of larger patches of prey).

Foraging strategies such as these facilitate continuous acquisition of food and help to minimize the need for reliance on energy stores to meet energetic requirements. A social system involving the communal care of young as observed in sperm whales (Mesnick *et al.* 2003) allows a mother the freedom to leave her calf at the surface to continuously forage during lactation, further facilitating the ability to continually acquire energy to meet the demands of reproduction, and thereby reducing the reliance on energy stores to

meet these energetic demands. A prolonged reproductive strategy resulting in large well developed young facilitates the ability for a mother to be mobile and therefore utilize a highly abundant, widely distributed prey group successfully, again allowing for the continual acquisition of energy. The ability to pass on energy acquired to ensure the survival and maximal fitness of offspring ensures continuation and success of the population.

However, the presence of individuals in these units unrelated to any other individuals in the unit is intriguing and presents a conundrum: why would individuals with no relation to others present such altruistic behaviour such as that observed in female sperm whale groups? The evolutionary advantages of a group existence include (i) increased vigilance and protection against predators and (ii) improved identification and utilization of food resources in the presence of scarce patchily distributed forage (Clark and Mangel 1986), both of which would serve to ensure maximal survival of individuals and their offspring. It is likely that the stability and relationships between individuals in these units are determined by finding a balance between the need to provide adequate protection from predators while still ensuring sufficient utilization of prey resources for each individual. This concept is not a novel one and has been discussed extensively elsewhere as part of density dependence theory (Clark and Mangel 1984, Kasuya 1991; Reznick *et al.* 2002), social foraging theory (Giraldeau and Caraco 2000) and within the theory of metapopulation dynamics (Holmes *et al.* 1994; Hanski 1998). Separation of the distribution of sexes in sperm whales has been postulated to be associated with a reduction in intraspecific competition for food resources (Best 1979). Female sperm whale units have been observed to merge with others temporarily in association with prey aggregations (Whitehead and Weilgart 2000). Dispersal of young males and some young females from natal units would serve to minimize the pressures associated with ensuring enough food for all within the unit.

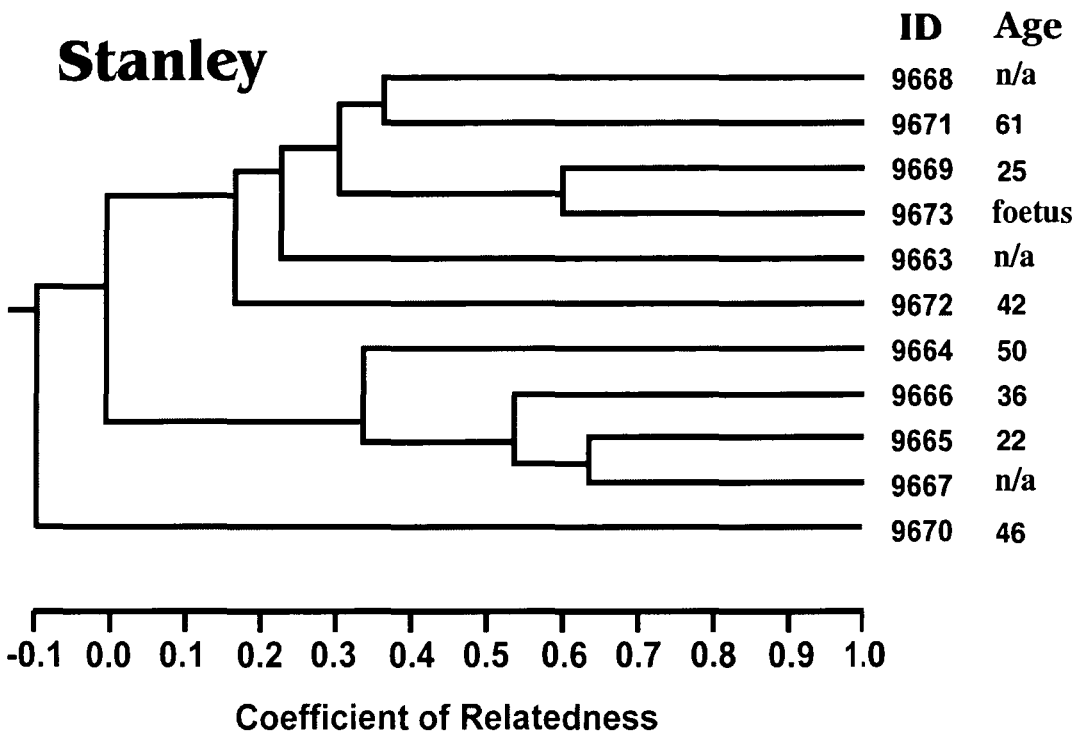


Figure 9.1. Relatedness among the ten adult females (and one foetus) that stranded at Stanley, Tasmania, in 1998. The strength of genetic relationships was calculated by estimating the probability of a microsatellite allele co-occurring in two different animals; higher values representing greater than average relatedness (Relatedness 5.0; Queller and Goodnight 1989). On this scale, first order relations (parents and offspring) would theoretically have a relatedness value of 0.5 (full siblings would have a mean value of 0.5); second order relations (grandparents and grandchildren, aunts/uncles and nieces/nephews or half siblings) would have a mean relatedness value of 0.25, and so on; observed values are distributed around these means. Individuals with high degrees of relatedness appear close to one another on the cluster diagram. Listed at the right are estimates of age based on the number of growth layer groups (GLG) identified in tooth sections (Chapter 2). UPGMA clustering was done using MEGA 1.01 (Kumar *et al.* 1993).

The results presented here are consistent for a mammal with a life history involving low fecundity, longevity, slow growth rates and attainment of sexual maturity, high input of resources into young over a protracted period and high sociality involving communal care of young and communal defense. These components function together to allow for individual flexibility within the constraints of the life history strategy of this species. This thereby allows individuals to adapt to changing environmental conditions and vary both behaviourally and physiologically in the acquisition and utilisation of energy resources and ultimately ensures survival of the individual and their offspring.

However, slow growth rates, late attainment of sexual maturity and low fecundity as demonstrated in sperm whales result in slow population growth. In a population close to carrying capacity, these life history traits are advantageous and minimise pressures on the population associated with competition for resources. However, in populations where a large proportion of the population is removed [current population estimates of sperm whales are in the order of only 32% of their original population (Whitehead 2002)], the ability to recover quickly is compromised and as a result, population growth is extremely slow. There are concerns that the low fecundity rate demonstrated by female sperm whales implies that post-whaling populations will not readily recover from decreases as a result of whaling. This suggests that unlike some species of previously exploited baleen whale populations in this region [*e.g.* humpback (*Megaptera novaeangliae*) and southern right whales (*Eubalaena australis*) which are estimated to be increasing in the order of 10 % and 8 % per annum respectively (Bannister *et al.* 1996; Burnell and McCulloch 2001)], post-whaling recovery of sperm whales is likely to be extremely slow (Whitehead and Weilgart 2000).

9.4. FUTURE RESEARCH DIRECTIONS

This study, as in all studies based on age-specific variables, assumed comparability of the estimated ages within this study to those estimated in other studies. Accurate age estimations in this species are near-impossible as a result of difficulties in the validation of age estimates, and this study highlighted the subsequent subjectivity of age determination in this species. The high subjectivity of age determination is of concern in making realistic comparative assessments between populations of sperm whales. Additionally, accuracy in age determination is imperative in the determination of age-specific demographic characteristics of populations. Compromises in the accuracy of calculated age-specific variables not only provide biased assessments of populations, they also limit the ability to evaluate changes in those variables both temporally and geographically. There is a need for research focusing on minimizing the subjectivity of age estimates in this species and increasing confidence in comparing age estimates between studies. The use of high quality photographs or other photographic techniques enabling clearer definition of dentinal growth layer groups should be investigated further as they may assist by increasing both intra- and inter-reader precision. Photographic techniques could be used to verify age estimates with other readers, ensuring interpretation of the same structures and facilitating 'consensus counts' generated by a number of readers. Additionally, means by which the effects of differential tooth wear on age estimates can be evaluated should be investigated. Monte Carlo randomizations such as those used in this study or alternative modeling methods may be methods by which more realistic population age structures can be attained.

The presence of males between the ages of 19 and 23 years in this study, the age structure of these groups and differences in the diet between sexes and age groups has highlighted our lack of knowledge of the dispersion patterns of juveniles from natal groups and the interactions between female groups and maturing male sperm whales. This study poses three questions for future research to consider: (1) do juvenile males disperse at older ages from natal groups in this region? (2) do juvenile males form associations with female groups after dispersal from natal groups? (3) what is the extent and nature of female dispersal from natal groups? Further genetic studies into these three groups may serve to provide greater insight into the issues these questions raise. Further a-field, progress in the application of satellite tracking techniques on large cetaceans (*e.g.* Watkins *et al.* 1999; Lagerquist *et al.* 2000; Heide-Jørgensen *et al.* 2001) may provide a means by which juvenile dispersion patterns and interactions between genders can be ascertained.

Further, the age structure of these groups and the calculation of survival rates for mature female sperm whales highlights our lack of knowledge on the status of this species in Australian waters. Future research aiming to establish the distribution and population status of this species in Australian waters should be encouraged. Recent research has identified areas of high upwelling along the southern Australian coastline (Gill 2002) and has identified this as not only a feeding area for blue whales (*Balenoptera musculus*), but many other cetacean species including sperm whales (P. Gill, pers. comm..). Previous studies on sperm whales in the Austrlian region coupled with data derived from whaling operations suggest that sperm whales are likely to seasonally inhabit and utilize southern Australian waters. Longitudinal studies incorporating regular aerial surveys may help to establish the extent and seasonality of this utilization and thus provide an indication of the distribution of stocks and population numbers of sperm whales in this region.

Commercial harvesting of cephalopods in the southern Australian area has been in operation periodically since 1972, targeting the Ommastrephids *N. gouldi, T. filippovae* and *O. bartrami* and the Sepioteuthid *Sepioteuthis australis*. While we now have an idea of the dietary requirements of adult female sperm whales in late summer in this region, we still have little information on temporal variations in dietary requirements or the dietary requirements of males and juveniles of both sexes. This information, coupled with information on the distribution and population numbers of sperm whales throughout this region is important in order to understand any potential competition, the distribution of this competition temporally and spatially and the impacts of such competition on cephalopod populations in this area. With the further documentation of fatty acid profiles of prey species, this technique may provide insights into the longer-term diet of these animals. The feasibility of novel dietary techniques such as fecal DNA analysis (Jarman *et al.* 2002) should also be considered as means by which we may be able to compliment hard-part remains dietary information.

Knowledge of the distribution, stock identity, numbers of sperm whales and critical habitats for this species in this region is essential in identifying both present and potential pressures on populations. This project has provided some insights into the basic biology and presence of pollutants in this species, and has identified primary confounding factors in the assessment of impacts associated with pollution in marine mammal species. It is clear that only with a more substantial understanding of the biology and ecology of this species will we be able to provide a more definitive assessment of the impacts of pollution on sperm whales in the Australian region. Further work should be expanded to additionally include the assessment of potential impacts from other areas, such as competition for fisheries and with the expanding use of oceanic resources, impacts associated with petroleum industries, noise, and shipping.

REFERENCES

A Geographical Information System (GIS) atlas of squid distribution in the Southern Ocean. (2001). http://www.nerc-bas.ac.uk/public/mlsd/squid-atlas/. British Antarctic Survey.

Ackman, R. G., Hingley, J. H., Eaton, C. A., Logan, V. H. and P. H. Odense. (1975a). Layering and tissue composition in the blubber of the northwest Atlantic sei whale (*Balaenoptera borealis*). Canadian Journal of Zoology 53: 1340-1344.

Ackman, R. G., Hingley, J. H. , Eaton, C. A. , Sipos, J. C. and E. D. Mitchell. (1975b). Blubber fat deposition in mysticeti whales. Canadian Journal of Zoology 53: 1332-1339.

Adrian, W. J. and M. L. Stevens. (1979). Wet *vs.* dry weights for heavy metal toxicity determinations in duck liver. Journal of Wildlife Diseases 15: 125-126.

Aguilar, A. (1983). Organochlorine pollution in sperm whales, *Physeter macrocephalus*, from temperate waters of the eastern North Atlantic. Marine Pollution Bulletin 14(9): 349-352.

Aguilar, A. (1984). Relationship of DDE/ΣDDT in marine mammals to the chronology of DDT input into the ecosystem. Canadian Journal of Fisheries and Aquatic Science 41: 840-844.

Aguilar, A. (1985). Compartmentation and reliability of sampling procedures in organochlorine pollution surveys of cetaceans. Residue Reviews 95: 91-114.

Aguilar, A. (1987). Using organochlorine pollutants to discriminate marine mammal populations: a review and critique of the methods. Marine Mammal Science 3(3): 242-262.

Aguilar, A. and A. Borrell. (1990). Patterns of lipid content and stratification in the blubber of fin whales (*Balaenoptera physalus*). Journal of Mammalogy 71(4): 544-554.

Aguilar, A. and A. Borrell. (1991). Heterogeneous distribution of organochlorine contaminants in the blubber of baleen whales: implications for sampling procedures. Marine Environmental Research 31: 275-286.

Aguilar, A. and A. Borrell. (1994a). Abnormally high polychlorinated biphenyl levels in striped dolphins (*Stenella coeruleoalba*) affected by the 1990-1992 Mediterranean epizootic. The Science of the Total Environment 154: 237-247.

Aguilar, A. and A. Borrell. (1994b). Assessment of organochlorine pollutants in cetaceans by means of skin and hypodermic biopsies. Pages 245-267 *in* M. C. Fossi and C. Leonzio (eds.). Non destructive biomarkers in vertebrates. Lewis Publishers, Boca Raton.

Aguilar, A., Borrell, A. and T. Pastor. (1999). Biological factors affecting variability of persistent pollutant levels in cetaceans. Journal of Cetacean Research and Management Special Issue 1: 83-116.

Aguilar, A., Borrell, A. and P. J. H. Reijnders. (2002). Geographical and temporal variation ion levels of organochlorine contaminants in marine mammals. *Marine Environmental Research* 53, 425-452.

Aguilar, A., Jover, L. and A. Borrell. (1993). Heterogeneities in organochlorine profiles of Faroese long-finned pilot whales: indication of segregation between pods? Report of the International Whaling Commission (special issue 14): 359-367.

Alexeyev, D. O. (1994). New data on the distribution and biology of squids from the Southern Pacific. Ruthenica 4(2): 151-166.

Allcock, L. and M. R. Clarke. (2001). CIAC beak database. Version 1.0. CD-ROM.

Ames, A. L. and E. S. Van Vleet. (1996). Organochlorine residues in the Florida manatee, *Trichechus manatus latirostris*. Marine Pollution Bulletin 32(4): 374-377.

Amos, B., Bloch, D., Desportes, G., Majerus, T. M. O., Bancroft, D. R., Barrett, J. A. and G. A. Dover. (1993). A review of molecular evidence relating to social organisation and breeding system in the long-finned pilot whale. Reports of the International Whaling Commission (special issue 14): 209-218.

Anas, R. E. (1970). Accuracy in assigning ages to fur seals. Journal of Wildlife Management 34(4): 844-852.

Anderson, G. R. V. (1991). Australia. Progress report on cetacean research, May 1989 to May 1990. Report of the International Whaling Commission 41: 223-229.

Arnbom, T. (1987). Individual identification of sperm whales. Report of the International Whaling Commission 37: 201-204.

Arnbom T, V. Papastavrou, L. S. Weilgart and H. Whitehead. (1987). Sperm whales react to an attack by killer whales. Journal of Mammalogy 68(2): 450-453.

Arnbom, T. and H. Whitehead. (1989). Observations on the composition and behaviour of groups of female sperm whales near the Galapagos Islands. Canadian Journal of Zoology 67: 1-7.

Ash, C. F. (1956). Variation in blubber thickness with length in fin whales. Norsk Hvalfangst-Tidende 10: 550-554.

Australian Fisheries Management Authority. (2001). Southern squid jig fishery bycatch action plan 2001. Australian Fisheries Management Authority. 7+iipp.

Bannister, J. L. (1969). The biology and status of the sperm whales off Western Australia- an extended summary of results of recent work. Reports of the International Whaling Commission 19: 70-76.

Bannister, J. L. (1974). Whale populations and current research off Western Australia. Pages 239-254 *in* W. E. Schevill (ed.). The whale problem. A status report. Harvard University Press, Cambridge.

Bannister, J. L. (1977). Sperm whales off Albany, Western Australia. Reports of the International Whaling Commission 27: 274-276.

Bannister, J. L., Kemper, C. M. and R. M. Warneke. (1996). The Action Plan for Australian Cetaceans. Australian Nature Conservation Agency, Canberra. 272pp.

Barlow, J. and P. Boveng. (1991). Modelling age-specific mortality for marine mammal populations. Marine Mammal Science 7(1): 50-65.

Barlow, J. and P. J. Clapham. (1997). A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology 78(2): 535-546.

Bedard, J. (1998). The use of dietary lipids as food web tracers in sperm whales (*Physeter macrocephalus*). Graduate diploma thesis, Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Hobart, Tasmania.

Béland, P., DeGuise, S., Girard, C., Lagacé, A., Martineau, D., Michaud, R., Muir, D. C. G., Norstrum, R. J., Pelletier, É., Ray, S. and L. R. Shugart. (1993). Toxic compounds and health and reproductive effects in St. Lawrence beluga whales. Journal of Great Lakes Research 19(4): 766-775.

Bell, C. M. (1997). Growth of the southern elephant seal *Mirounga leonina* (Linnaeus 1758) at Macquarie Island. MSc thesis. University of Tasmania.

Berzin, A. A. (1972). The sperm whale. Pacific Scientific Research Institute of Fisheries and Oceanography, Moscow. (Translated from Russian by the Israel Program for Scientific Translations, No. 600707, Jerusalem, 1972). 387pp.

Best, N. J., Bradshaw, C. J. A., Hindell, M. A. and P. D. Nichols. (2003). Vertical stratification of fatty acids in the blubber of southern elephant seals (*Mirounga leonina*): implications for diet analysis. Comparative Biochemistry and Physiology B. 134: 253-263.

Best, P. B. (1968). The sperm whale (*Physeter catadon*) off the west coast of South Africa. 2. Reproduction in the female. Investigational Reports of the Division of Sea Fisheries of South Africa 66: 1-32.

Best, P. B. (1970). The sperm whale (*Physeter catadon*) off the west coast of South Africa. 5. Age, growth and mortality. Investigational Reports of the Division of Sea Fisheries of South Africa 79: 1-27.

Best, P. B. (1976). Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin (*Lagenorhynchus obscurus*). South African Journal of Science 72: 216-218.

Best, P. B. (1979). Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 *in* H. E. Winn and B. L. Olla (eds.). Behaviour of marine animals. Current perspectives in research 3. Plenum Press, N.Y.

Best, P. B., A. S. Canham and N. MacLeod. (1984). Patterns of reproduction in sperm whales, *Physeter macrocephalus*. Report of the International Whaling Commission (Special Issue 6): 51-79.

Bjørge, A., Hohn, A. A., Kvam, T., Lockyer, C., Schweder, T. and H. Aarefjord. (1995). Report of the harbour porpoise age determination workshop, Oslo, 21-23 May 1990. Report of the International Whaling Commission (special issue) 16: 477-496.

Bloch, D., Lockyer, C. and M. Zachariassen. (1993). Age and growth parameters of the log-finned pilot whale off the Faroe Islands. Reports of the International Whaling Commission (special issue 13): 163-208.

Boness, D. J., P. J. Clapham, and S. L. Mesnick. (2002). Life history and reproductive strategies. Pages 278-324 *in* A. R. Hoelzel (ed.). Marine mammal biology. An evolutionary approach. Blackwell Science Ltd., Oxford.

Borrell, A. (1993). PCB and DDTs in blubber of cetaceans from the northeastern North Atlantic. Marine Pollution Bulletin 26(3): 146-151.

Borrell, A. and A. Aguilar. (1993). DDT and PCB pollution in blubber and muscle of long-finned pilot whales from the Faroe Islands. Report of the International Whaling Commission (Special Issue 14): 351-358.

Borrell, A. and A. Aguilar. (1999). A review of organochlorine and metal pollutants in marine mammals from Central and South America. Journal of Cetacean Research and Management Special Issue 1: 195-207.

Bow, J. M. and C. Purday. (1966). A method of preparing sperm whale teeth for age determination. Nature 210: 437-438.

Boyce, M. S. (1984). Restitution of r- and K-selection as a model of density dependent natural selection. Annual Review in Ecology and Systematics 15: 427-447.

Boyd, I. L. and T. S. McCann. (1989). Pre-natal investment in reproduction by female Antarctic fur seals. Behavioural Ecology and Sociobiology 24: 377-385.

Brault, S. and H. Caswell. (1993). Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74(5): 1444-1454.

Bradshaw, C. J. A., Hindell, M. A., Best, N. J., Phillips, K. L., Wilson, G. and Nichols, P. D. (In Press). You are what you eat: describing the foraging ecology of elephant seals (Mirounga leonina) using blubber fatty acids. Proceedings of the Royal Society of London B. Biological Science: TBA

Brodie, P. F., Geraci, J. W. and D. J. St. Aubin. (1990). Dynamics of tooth growth in beluga whales, *Delphinapterus leucas*, and effectiveness of tetracycline as a marker for age determination. Pages 141-148 *in*: T. G. Smith, D. J. St Aubin and J. R. Geraci (eds.). Advances in Research on the Beluga Whale, Delphinapterus leucas. Canadian Bulletin of Fisheries and Aquatic Science 224, Department of Fisheries and Oceans, Ottawa.

Brodie, P. F. and A. J. Påsche. (1982). Density-dependent condition and energetics of marine mammal populations in multispecies fisheries management. Canadian Journal of Fisheries and Aquatic Science (Special Issue 59): 35-38.

Brown, S. G. (1981). Movements of marked sperm whales in the Southern Hemisphere. Reports of the International Whaling Commission 31: 835-837.

Burnell, S. R. and R. E. McCulloch. (2001). Draft recovery plan for southern right whales in Australian waters. Environment Australia, Canberra. 47 pp.

Caswell, H. (2001). Matrix population models: cpnstruction, analysis and interpretation. Sinauer Associates, Sunderland. 722+xxii pp.

Caughley, G. (1977). Analysis of vertebrate populations. John Wiley and Sons, Chichester. 234+ix pp.

Caughley, G. and A. R. E. Sinclair. (1994). Wildlife ecology and management. Blackwell Science, Cambridge. 334+x pp.

Cephbase: a database-driven web site on all living cephalopods (octopus, squid, cuttlefish and nautilus). (2002). http://www.cephbase.utmb.edu/.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Science 39: 1208-1210.

Childerhouse, S. J., Dawson, S. M. and E. Slooten. (1995). Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. Canadian Journal of Zoology 3: 723-731.

Choquenot, D. (1991). Density-dependent growth, body condition and demography in feral donkeys: testing the food hypothesis. Ecology 72: 805-813.

Christal, J. and H. Whitehead. (2001). Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107: 323-340.

Christensen, I. (1990). A note on recent strandings of sperm whales (*Physeter macrocephalus*) and other cetaceans in Norwegian waters. Report of the International Whaling Commission 40: 513-515.

Clapham, P. J. and L. T. Hatch. (2000). Determining spatial and temporal scales for population management units: lessons from whaling. Paper SC/52/SD2 presented to the Scientific Committee of the International Whaling Commission. 10pp.

Clarke, A., Clarke, M. R., Holmes, L. J. and Waters, T. D. (1985). Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). Journal of the Marine Biological Association of the United Kingdom 65: 983-986.

Clark, C. W. and M. Mangel. (1986). The evolutionary advantages of group foraging. Theoretical Population Biology 30: 45-75.

Clarke, M. R. (1966) . A review of the systematics and ecology of oceanic squids. Advances in Marine Biology 4: 91-300.

Clarke, M. R. (1980). Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. Discovery Reports 37: 1-324.

Clarke, M. R. (1983). Cephalopod biomass - estimation from predation. Memoirs of the National Museum, Victoria 44: 95-107.

Clarke, M. R. (ed.). (1986) A handbook for the identification of cephalopod beaks. Oxford University Press, Oxford. 273+xiiipp.

Clarke, M. R. (1996) Cephalopods as prey. III. Cetaceans. Philosophical Transactions of the Royal Society of London B 351: 1053-1065.

Clarke, M. R. and MacLeod, N. (1974) Cephalopod remains from a sperm whale caught off Vigo, Spain. Journal of the Marine Biological Association of the United Kingdom 54: 959-968.

Clarke, M. R. and MacLeod, N. (1976). Cephalopod remains from sperm whales caught off Iceland. Journal of the Marine Biological Association of the United Kingdom 56: 733-749.

Clarke, M. R. and MacLeod, N. (1982). Cephalopod remains from the stomachs of sperm whales caught in the Tasman Sea. Memoirs of the National Museum, Victoria 43: 25-42.

Clarke, M. R., MacLeod, N., Castello, H. P. and M. C. Pinedo. (1980). Cephalopod remains from the stomach of a sperm whale stranded at Rio Grande do Sul in Brazil. Marine Biology 59: 235-239.

Clarke, M. R., Macleod, N. and O. Paliza. (1976). Cephalopod remains from the stomachs of sperm whales caught off Peru and Chile. Journal of Zoology, London 180: 477-493.

Clarke, M. R. and M. A. C. Roeleveld. (1998). Cephalopods in the diet of sperm whales caught commercially off Durban, South Africa. South African Journal of Marine Science 20: 41-45.

Clarke, M. R. and C. F. E. Roper. (1998) Cephalopods represented by beaks in the stomach of a sperm whale stranded at Paekakariki, North Island, New Zealand. South African Journal of Marine Science 20: 129-133.

Clarke, M. and R. Young. (1998). Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. Journal of the Marine Biological Association of the United Kingdom 78: 623-641.

Clarke, R. and O. Paliza. (1972). Sperm whales of the southeast Pacific. Part III. Morphometrics. Hvalrådets Skrifter 53: 1-106.

Clarke R., Paliza, O. and L. A. Aguayo. (1988). Sperm whales in the southeast Pacific. Part IV: fatness, food and feeding. Investigations on Cetacea 21: 53-195.

Clarke, R., A. Aguayo L. and O. Paliza. (1968). Sperm whales of the southeast Pacific. Part I: Introduction. Part II: Size range, external characters and teeth. Hvalrådets Skrifter 51:1-80.

Cockcroft, V.G. and G.J.B. Ross. (1989). Age, growth and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of Southern Africa. Fishery Bulletin 88: 289-302.

Cockcroft, V. G. and G. J. B. Ross. (1991). Occurrence of organochlorines in stranded cetaceans and seals from the east coast of southern Africa. UN Environmental Program: 271-276.

Collins, M. A., Yau, C., Allcock, L. and Thurston, M. H. (2001). Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom 81: 105-117.

Croxall, J. P. and Prince, P. A. (1982). Calorific content of squid (Mollusca: Cephalopoda). British Antarctic Survey Bulletin 55: 27-31.

de Kock, A. C., Best, P. B., Cockcroft, V. and C. Bosma. (1994). Persistent organochlorine residues in small cetaceans from the east and west coasts of southern Africa. The Science of the Total Environment 154: 153-162.

DeLong, R. L., Antonelis, G. A., Oliver, C. W., Stewart, B. S., Lowry, M. C. and P. K. Yochem. (1991). Effects of the 1982-83 El Niño on several population parameters and diet of California sea lions on the California Channel Islands. Pages 166-172 *in* F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Responses to environmental stress. Springer-Verlag, Berlin.

Donovan, G. P. (1985). A brief review of aging techniques for toothed cetaceans within the context of marine parks. Proceedings of the Symposium on Endangered Marine Animals and Marine Parks 1: 84-92.

Donovan, G. P., Breiwick, J. and J. L. Bannister. (1982). A note on comparative readings of sperm whale teeth. Reports of the International Whaling Commission 32: 251-252.

Doubleday, W. G. and W. D. Bowen. (1980). Inconsistencies in reading the age of harp seal (*Pagophilus groenlandicus*) teeth, their consequences and a means of reducing resulting biases. NAFO SCR Doc. 80/XI/160. Northwest Atlantic Fisheries Organisation. 24 pp.

Dufault, S., Whitehead, H. and M. Dillon. (1999). An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) woldwide Journal of Cetacean Research and Management 1(1): 1-10.

Duinker, J. C. and M. T. J. Hillebrand. (1979). Mobilization of organochlorines from female lipid tissue and transplacental transfer to fetus in a harbour porpoise (*Phocoena phocoena*) in a contaminated area. Bulletin of Environmental Contamination and Toxicology 23: 728-732.

Dunning, M. (1985). General patterns in the summer distribution of early juvenile ommastrephid squid off eastern Australia (Mollusca, Cephalopoda). Vie Milieu 35(3/4): 163-168.

Dunning, M. C. (1988). Distribution and comparative life history studies of deepwater squid of the family Ommastrephidae in Australasian waters. PhD thesis. Zoology Department, University of Queensland, St. Lucia. 288+xixpp.

Dunning, M. C. (1993). Summer populations of *Ommastrephes bartramii* (Lesuer, 1821) and *Todarodes filippovae* Adam, 1975 (Cephalopoda: Ommastrephidae) from the Tasman Sea. Pages 97-118 *in* T. Okatani, R. K. O'dor and T. Kubodera (eds.). Recent advances in fisheries biology. Tokai University Press, Tokyo.

Dunning, M. C. (1998). An overview of the fisheries biology and resource potential of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) in the Southern Hemisphere. Pages 65-76 *in* T. Okutani (ed.). Contributed papers to international symposium on large pelagic squids. Japan Marine Fishery Resources Research Centre, Tokyo.

Dunning, M. and Brandt, S. B. (1985). Distribution and life history of deep-water squid of commercial interest from Australia. Australian Journal of Marine and Freshwater Research 36: 343-359.

Evans, K. (In Press). Pollution and marine mammals in the Southern Hemisphere. Present or potential threat? Pages TBA *in* N. J. Gales, M. A. Hindell and R. Kirkwood (eds.). Marine mammals. Fisheries, tourism and management issues. CSIRO Publishing, Melbourne.

Evans, P. G. H. (1997). Ecology of sperm whales (*Physeter macrocephalus*) in the eastern North Atlantic, with special reference to sightings and strandings records from the British Isles. Bulletin de l'Institut des Sciences Naturelles de Belgique 67(supplement): 37-46.

Ferrero, R. C. and W. A. Walker. (1999). Age, growth and reproductive patterns of Dall's porpoise (*Phocoenoides dalli*) in the central north Pacific Ocean. Marine Mammal Science 15(2): 273-313.

Fiscus, C. H., Rice, D. W. and A. A. Wolman. (1989). Cephalopods from the stomachs of sperm whales taken off California. NOAA Technical Report, NMFS 83. US Department of Commerce, Seattle. 12pp.

Fredheim, B., Holen, S., Ugland, K. I., and O. Grahl-Nielsen. (1995). Fatty acid composition in blubber, heart and brain from phocid seals. Pages 153-168 *in* A. S. Blix, L. Walløe and Ø. Ulltang (eds.). Whales, seals, fish and man. Elsevier Science, B. V.

Fujiwara, M. and H. Caswell. (2001). Demography of the endangered North Atlantic right whale. Nature 414: 537-541.

Gallagher, M. D. (1991). Strandings of sperm whales (*Physeter macrocephalus*) on the shores of Oman, Eastern Arabia. Pages 241-245 *in* S. Leatherwood and G. P. Donovan (eds.). Cetaceans and cetacean research in the Indian Ocean Sanctuary. Marine Mammal Technical Report Number 3, U.N. Environment Programme Nairobi, Kenya.

Gambell, R. (1972). Sperm whales off Durban. Discovery Reports 35: 199-358.

Gambell, R. (1977). Dentinal layer formation in sperm whale teeth. Pages 583-590 *in* M. Angel (ed.). A Voyage of Discovery. Pergamon Press, Oxford.

Gaskin, D. E. (1973). Sperm whales in the western South Pacific. New Zealand Journal of Marine and Freshwater Research 7(1&2): 1-20.

Gaskin, D. E. and M. W. Cawthorn. (1967). Diet and feeding habits of the sperm whale (*Physeter catadon* L.) in the Cook Strait region of New Zealand. New Zealand Journal of Marine and Freshwater Research 2: 156-179.

Geraci, J. R. and V. J. Lounsbury. (1993). Marine mammals ashore: a field guide for strandings. Texas A&M University Sea Grant College Program Publication, Galveston, Texas. 305+xipp.

Gill, P. C. (2002). A blue whales (*Baleanoptera musculus*) feeding ground in a southern Australian coastal upwelling zone. Journal of Cetacean Research and Management 4(2):179-184.

Giraldeau, L-A and T. Caraco. (2000). Social foraging theory. Princeton University Press, Princeton. 362+xiii pp.

González, A. F., López, A., Guerra, A. and A. Barreiro. (1994). Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fisheries Research 21: 179-191.

Gordon, J. (1987). The behaviour and ecology of sperm whales off Sri Lanka. PhD thesis, Darwin College, Cambridge. 347 pp.

Goren, A. D., Brodie, P. F., Spotte, S., Ray, G. C., Kaufman, H. W., Gwinnett, A. J., Sciubba, J. J. and J. D. Buck. (1987). Growth layer groups (GLGs) in the teeth of adult belukha whale (*Delphinapterus leucas*) of known age: evidence of two annual layers. Marine Mammal Science 3(1): 14-21.

Guiler, E. R. (1978). Whale strandings in Tasmania since 1945 with notes on some seal reports. Papers and Proceedings of the Royal Society of Tasmania 112: 189-213.

Guinet, C., Roux, J. P., Bonnet, M. and V. Mison. (1998). Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. Canadian Journal of Zoology 76: 1418-1424.

Guitart, R., X. Guerrero, A.M. Silvestre, J.M. Gutiérrez and R. Mateo. (1996). Organochlorine residues in tissues of striped dolphins affected by the 1990 Mediterranean epizootic: relationships with fatty acid composition. Archives of Environmental Contamination and Toxicology 30: 79-83.

Gurevich, V. S., Stewart, B. S. and L. H. Cornell. (1980). The use of tetracycline in age determination of common dolphins, *Delphinus delphis*. Report of the International Whaling Commission (special issue 3): 165-169.

Hanks, J. (1981). Characterisation of population condition. Pages 47-73 *in* C. W. Fowler and T. D. Smith (eds.). Dynamics of large mammal populations. John Wiley and Sons Inc., New York.

Hanski, I. (1998). Metapopulation dynamics. Nature 396: 41-49.

Harrison Matthews, L. (1938). The sperm whale, *Physeter catadon*. Discovery Reports 17: 93-168.

Harvey, P. H. and A. F. Read. (1985). How and why do mammalian life histories vary? Pages 213-233 in M. S. Boyce (ed.). Evolution of life histories of mammals. Theory and Pattern. Yale University Press, New Haven.

Hatanaka, H., Kawahara, S. and Y. Uozumi. (1985). Comparison of life cycles of five Ommastrephid squids fished by Japan: *Todarodes pacificus, Illex illecebrosus, Illex argentinus, Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. NAFO Scientific Council Studies 9: 59-68.

Heide-Jørgensen, M. P., Kleivane, L., Øien, N., Laidre, K. L. and M. Villum Jensen. (2001). A new technique for deploying satellite transmitters on baleen whales: tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. Marine Mammal Science 17(4): 949-954.

Henry, J. and P. B. Best. (1983). Organochlorine residues in whales landed at Durban, South Africa. Marine Pollution Bulletin 14(6): 223-227.

Hohn, A. A. (1980). Analysis of growth layers in the teeth of *Tursiops truncatus*, using light microscopy, microradiography, and SEM. Report of the International Whaling Commission (special issue) 3: 155-160.

Hohn, A. A. (1990). Reading between the lines: analysis of age estimation in dolphins. Pages 575-584 *in*: S. Leatherwood and R. R. Reeves (eds.). The Bottlenose Dolphin. Academic Press, San Diego.

Hohn, A. A. and S. Fernandez. (1999). Biases in dolphin age structure due to age estimation technique. Marine Mammal Science 15(4): 1124-1132.

Hohn, A. A., Scott, M. D., Wells, R. S., Sweeney, J. C. and A. B. Irvine. (1989). Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Marine Mammal Science 5(4): 315-342.

Holmes, E. E., Lewis, M. A., Banks, J. E. and R. R. Veit. (1994). Partial differential equations in ecology: spatial interactions and population dynamics. Ecology 75(1): 17-29.

Holsbeek, L., Joiris, C. R. Debacker, V., Ali, I. B., Roose, P., Nellissen, J., Gobert, S., Bouquegneau, J. and M. Bossicart. (1999). Heavy metals, organochlorines and polycyclic aromatic hydrocarbons in sperm whales stranded in the southern North Sea during 1994/1995 winter. Marine Pollution Bulletin 38(4): 304-313.

Hooker, S. K., Iverson, S. J., Ostrom, P. and S. C. Smith. (2001). Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Canadian Journal of Zoology 79: 1442-1454.

Hui, C. A. (1980). Variability of dentin deposits in *Tursiops truncatus*. Canadian Journal of Fisheries and Aquatic Science 37: 712-716.

Imber, M. J. (1978). The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidea) in the New Zealand region. New Zealand Journal of Zoology 5: 445-484.

International Whaling Commission. (1967). Report of the Scientific Committee. Appendix E. Sperm whale sub-committee meeting report. Report of the International Whaling Commission 17: 120-127.

International Whaling Commission. (1969). Report of the Scientific Committee. Appendix H. Report of the meeting on age determination in whales. Report of the International Whaling Commission 19: 131-137.

International Whaling Commission. (1971). Annex D. Report of the special meeting on sperm whale biology and stock assessments. Report of the International Whaling Commission 21: 42-50.

Iverson, S. J. (2002). Blubber. Pages 107-112 *in* W. F. Perrin, B. Würsig and J. G. M. Thewissen (eds.). Encyclopedia of marine mammals. Academic Press, San Diego.

Iwata, H., Tanabe, S., Sakai, N. and R. Tatsukawa. (1993). Distribution of persistent organochlorines in the oceanic air and surface seawater and the role of the ocean on their global transport and fate. Environmental Science and Technology 27: 1080-1098.

Jackson, G. D., Buxton, N. G. and George, M. J. A. (1997). Beak length analysis of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) from the Falklands Islands region of the Patagonian shelf. Journal of the Marine Biological Association of the United Kingdom 77: 1235-1238.

Jackson, D., Shaw, A. G. P. and C. Lalas. (2000). Distribution and biomass of two squid species off southern New Zealand: *Nototodarus sloanii* and *Moroteuthis ingens*. Polar Biology 23: 699-705.

Jaquet, N., Dawson, S. and E. Slooten. (2000). Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. Canadian Journal of Zoology 78: 407-419.

Jaquet, N. and H. Whitehead. (1996). Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135: 1-9.

Jarman, S. N., Gales, N. J., Tierney, M., Gill, P. C. and N. G. Elliot. (2002). A DNA based method for the identification of krill species. Application to analysisng the diet of marine vertebrate predators. Molecular Ecology: 2670-2690.

Jauniaux, T., Brosens, L., Jacquinet, E., Lambrigts, D. and F. Coignoul. (1997). Pathological investigations on sperm whales stranded on the Belgian and Dutch coasts. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 67(supplement): 63-67.

Jefferson, T. A., P. J. Stacey and R. W. Baird. (1991). A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Review 21(4): 151-180.

Jepson, P.D., Bennett, P. M., Allchin, C. R., Law, R. J., Kuiken, T., Baker, J.R., Rogan, E. and J. K. Kirkwood. (1999). Investigating potential associations between chronic exposure to polychlorinated biphenyls and infectious disease mortality in harbour porpoises from England and Wales. The Science of the Total Environment 243/244: 339-348.

Johnston, P. A., Stringer, R. L. and D. Santillo. (1996). Cetaceans and environmental pollution: the global concerns. Pages 219-261 *in* M. P. Simmonds and J. D. Hutchinson (eds.). The conservation of whales and dolphins'. John Wiley and Sons Ltd. Chichester.

Joiris, C.R., L. Holsbeek, M. Bossicart and G. Tapia. (1997). Mercury and organochlorines in four sperm whales stranded on the Belgian coast, November 1994. Bulletin de L'Institut Royal des Sciences Naturelles de Belgique 67 - supplement: 69-74.

Jönssen, I. (1997). Capital and income breeding as alternative tactics of resource used in reproduction. Oikos 78: 57-66.

Kannan, N., Tanabe, S., Ono, M. and R. Tatsukawa. (1989). Critical evaluation of the polychlorinated biphenyl toxicity in terrestrial and marine mammals: increasing impact of non-ortho and mono-ortho coplanar polychlorinated biphenyls from land to ocean. Archives of Environmental Contamination and Toxicology 18: 850-857.

Kasuya, T. (1991). Density dependent growth in North Pacific sperm whales. Marine Mammal Science 7(3): 230-257.

Kasuya, T. Examination of the reliability of catch statistics in the Japanese coastal sperm whale fishery. Journal of Cetacean Research and Management 1(1): 109-122.

Kawai, S., Fukushima, M., Miyazaki, N. and R. Tatsukawa. (1988). Relationship between lipid composition and organochlorine levels in the tissues of striped dolphin. Marine Pollution Bulletin 19(3): 129-133.

Kawakami, T. (1980). A review of sperm whale food. Scientific Reports of the Whales Research Institute 32: 199-218.

Kemper, C., Gibbs, P., Obendorf, D., Marvanek, S. and C. Lenghaus. (1994). A review of heavy metal and organochlorine levels in marine mammals in Australia. The Science of the Total Environment 154: 129-139.

Kirkwood, G. P., Allen , K. R. and J. L. Bannister. (1980). An assessment of the sperm whale stock subject to Western Australia catching. Reports of the International Whaling Commission (Special Issue 2): 147-150.

Kirkwood, G. P. and J. L. Bannister. (1980). Revised abundance indices for sperm whales off Albany, Western Australia. Reports of the International Whaling Commission (Special Issue 2): 89-92.

Klem, A. (1935). Contributions to the study of whale oils. Studies in the biochemistry of whale oils. Hvalradets Skrifter 11: 49-108.

Klevezal', G. A. (1980). Layers in the hard tissues of mammals as a record of growth rhythms of individuals. Report of the International Whaling Commission (special issue 3): 89-94.

Klevezal', G. A. and A. C., Myrick. (1984). Marks in the tooth dentine of female dolphins (Genus *Stenella*) as indicators of parturition. Journal of Mammalogy 65(1): 103-110.

Koopman, H. N. (1998). Topographical distribution of the blubber of harbour porpoises (*Phocoena phocoena*). Journal of Mammalogy 79(1): 260-270.

Koopman, H. N., Iverson, S. J. and D. E. Gaskin. (1996). Stratification and age-related differences in blubber fatty acids of the male harbour porpoise (*Phocoena phocoena*). Journal of Comparative Physiology B 165: 628-639.

Korzun, Y. V., Nesis, K. N., Nigmatullin, Ch. M. Ostapenko, A. A. and M. A. Pinchukov. (1979). New data on the distribution of squids, Family Ommastrephidae in the world ocean. Oceanology 19(4): 472-475.

Kumar, S., Tamura, K. and M. Nei. (1993). MEGA: Molecular evolutionary genetics analysis, version 1.0. Pennsylvania State University, Pennsylvania.

Lagerquist, B. A., Stafford, K. M. and B. R. Mate. (2000). Dive characteristics of satellite-monitored blue whales (*Balaenoptera musculus*)off the central Californian coast. Marine Mammal Science 16(2): 375-391.

Laird, A. K. (1969). The dynamics of growth. Research/Development August 1969: 28-31.

Langvatn, R. (1995). Age determination of mammals – some aspects of biochemistry and physiological mechanisms relating to deposition of incremental lines in dental tissues. Report of the International Whaling Commission (special issue 16): 499-510.

Law, R. J., Stringer, R. L., Allchin, C. R. and B. R. Jones. (1996). Metals and organochlorines in sperm whales (*Physeter macrocephalus*) stranded around the North Sea during the 1994/1995 winter. Marine Pollution Bulletin 32(1): 72-77.

Laws, R. M. (1952). A new method of age determination for mammals. Nature 169: 972-974.

Lipinski, M. R. (1993). Description of mature males of the Histioteuthid cephalopod *Histioteuthis atlantica* (Hoyle 1885) (Cephalopoda: Oegopsida) from the South Atlantic Ocean. South African Journal of Marine Science 13: 51-62.

Lockyer, C. (1977). Observations on diving behaviour of the sperm whale *Physeter catadon*. Pages 591-609 *in* M. V. Angel (ed.). A voyage of discovery. Pergamon Press, Oxford.

Lockyer, C. (1978). A theoretical approach to the balance between growth and food consumption in fin and sei whales, with special reference to the female reproductive cycle. Reports of the International Commission 28: 243-249.

Lockyer, C. (1980). Age determination studies on *Physeter macrocephalus*. Report of the International Whaling Commission (special issue) 3: 216.

Lockyer, C. (1981a). Growth and energy budgets of large baleen whales from the Southern Hemisphere. Mammals in the sea, FAO. Fisheries Series Number 5 Volume 3: 379-487.

Lockyer, C. (1981b). Estimates of growth and energy budget for the sperm whale, *Physeter catadon*. Pages 489-504 *in* Mammals in the seas. FAO. Fisheries Series Number 5 Volume 3. FAO, Rome.

Lockyer, C. (1986). Body fat condition in Northeast Atlantic fin whales *Balaenoptera physalus* and it's relationship with reproduction and food resource. Canadian Journal of Fisheries and Aquatic Science 43: 142-147.

Lockyer, C. (1987). Evaluation of the role of fat reserves in relation to the ecology of north Atlantic fin and sei whales. Pages 183-203 *in* A.C. Huntley, D. P. Costa, A. J. Worthy, M. A. Castellini (eds). Approaches to marine mammal energetics. Marine Mammal Society Special Publication 1.

Lockyer, C. (1991). Body composition of the sperm whale, *Physeter catadon*, with special reference to the possible functions of fat depots. Rit Fiskideildar 12(2): 1-24.

Lockyer, C. (1993a). A report on patterns of deposition of dentine and cement in teeth of pilot whales, genus *Globicephala*. Report of the International Whaling Commission (special issue) 14: 137-161.

Lockyer, C. (1993b). Seasonal changes in body fat condition of northeast Atlantic pilot whales, and their biological significance. Report of the International Whaling Commission (special issue 14): 325-350.

Lockyer, C. (1995a). A review of factors involved in zonation in odontocete teeth, and an investigation of the likely impact of environmental factors and major life events on harbour porpoise tooth structure. Report of the International Whaling Commission (special issue) 16: 511-529.

Lockyer, C. (1995b). Aspects of the morphology, body fat condition and biology of the harbour porpoise, *Phocoena phocoena*, in British waters. Report of the International Whaling Commission (special issue 16): 199-209.

Lockyer, C. and S. G. Brown. (1981). The migration of whales. Pages 105-137 *in* D. J. Aidley (ed.). Society for Experimental Biology Seminar Series. 13. Animal Migration. Cambridge University Press, Cambridge.

Lockyer, C. H., McConnell, L. C. and T. D. Waters. (1984). The biochemical composition of fin whale blubber. Canadian Journal of Zoology 62: 2553-2562.

Lockyer, C. H., McConnell, L. C. and T. D. Waters. (1985). Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Canadian Journal of Zoology 63: 2328-2338.

Lordan, C., Collins, M. A. and C. Perales-Raya. (1998). Observations on morphology, age and diet of three *Architeuthis* caught off the west coast of Ireland in 1995. Journal of the Marine Biological Association of the United Kingdom 78: 903-917.

Lu, C. C. and R. Ickeringill. (2002). Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. Museum Victoria Science Reports 5. Museum Victoria, Melbourne.

Lu, C. C. and R. Williams. (1994). Contribution to the biology of squid in Prydz Bay region, Antarctica. Antarctic Science 6(2): 223-229.

Luckas, B., Vetter, W. Fischer, P., Heidmann, G. and J. Plötz. (1990). Characteristic chlorinated hydrocarbon patterns in the blubber of seals from different marine regions. Chemosphere 21(1-2): 13-19.

Lunn, N. J. and I. L. Boyd. (1993). Effects of maternal age and condition on parturition and the preinatal period of Antarctic fur seals. Journal of Zoology, London 229: 55-67.

Lunn, N. J., Boyd, I. L. and J. P. Croxall. (1994). Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology 63: 827-840.

Lyrholm, T., Leimar, O., Johanneson, B. and U. Gyllesten. (1999). Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. Proceedings of the Royal Society of London. B. 266: 347-354.

Manly, F. J. (1997). Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London. 399+xix pp.

Martin, A. R. and M. R. Clarke. (1986). The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. Journal of the Marine Biological Association of the United Kingdom 66: 779-790.

Martineau, D., De Guise, S., Fournier, M., Shugart, L., Girard, C., Lagacé, A. and P. Béland. (1994). Pathology and toxicology of beluga whales from the St. Lawrence Estuary, Quebec, Canada. Past, present and future. The Science of the Total Environment 154: 201-215.

Masaki, Y. (1980). On the pregnancy rate of North Pacific sperm whales. Reports of the International Whaling Commission (Special Issue 2): 43-48.

McManus, T. J., Wapstra, J. E., Guiler, E. R., Munday, B. L. and D. L. Obendorf. (1984). Cetacean strandings in Tasmania from February 1978 to May 1983. Papers and Proceedings of the Royal Society of Tasmania 118: 117-135.

McSweeny, E. S. (1970). Description of the juvenile form of the Antarctic squid *Mesonychoteuthis hamiltoni* Robson. Malacologia 10(2): 323-332.

McSweeny, E. S. (1976). Systematics and morphology of the Antarctic cranchiid squid *Galiteuthis glacialis* (Chun). Biology of the Antarctic seas. VII: 1-39.

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. Behavioural and Brain Sciences 24(2): 346-347.

Mesnick, S. L., Evans, K. Taylor, B. L., Hyde, J., Escorza-Treviño, S., and A. E. Dizon. (2003). Sperm whale social structure: why it takes a village to raise a child. Pages 170-174 *in* B. M. d. Wall and P. L. Tyack (eds.). Animal social complexity. Intelligence, culture and individualized societies. Harvard University Press, New York.

Mikhalev, Y. A. (1982). Subjective and objective assessments of the laminations in sperm whale teeth. Report of the International Whaling Commission 32: 227-233.

Mikhalev, Y. A., Savusin, V. P., Kishiyan, N. A. and M. V. Ivashin. (1981). To the problem of feeding of sperm whales from the Southern Hemisphere. Reports of the International Whaling Commission 31: 737-745.

Minh, T. B., Nakata, H., Watanabe, M., Tanabe, S., Miyazaki, N., Jefferson, T. A., Prudente, M. and A. Subramanian. (2000). Isomer-specific accumulation and toxic assessment of polychlorinated biphenyls, including coplanar congeners, in cetaceans from the North Pacific and Asian coastal waters. Archives of Environmental Contamination and Toxicology 39: 398-410.

Moriarty, F. (1984). Persistent contaminants, compartmental models and concentration along food chains. Ecological Bulletins 36: 35-45.

Moss, C. J. (2001). The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. Journal of Zoology, London 255: 145-156.

Murphy, P. G. (1972). Sulfuric acid cleanup of animal tissues for analysis of acid-stable chlorinated hydrocarbon residues. Journal of the AOAC 55(6): 1360-1362.

Myrick, A. C. (1988). Is tissue resorption and replacement in permanent teeth of mammals caused by stress-induced hypocalcaemia? Pages 379-389 *in*: Z. Davidovitch (ed.). The Biological Mechanisms of Tooth Eruption and Root Resorption. EBSCO Media, Birmingham.

Myrick, A. C. (1991). Some new and potential uses of dentinal layers in studying delphinid populations. Pages 251-279 *in* K. Pryor and K. S. Norris (eds.). Dolphin societies: discoveries and puzzles. University of California Press, Oxford.

Myrick, A. C. and L. H. Cornell. (1990). Calibrating dental layers in captive bottlenose dolphins from serial tetracycline labels and tooth extractions. Pages 587-607 *in*: S. Leatherwood and R. R. Reeves (eds.). The Bottlenose Dolphin. Academic Press, San Diego.

Myrick, A. C., Hohn, A. A., Sloan, P. A., Kimura, M. and D. D. Stanley. (1983). Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. NOAA Technical Memorandum. NOAA-TM-NMFS-SWFC-30. 22 pp.

Myrick, A. C., Shallenbeger, E. W., Kang, I. and MacKay, D. B. (1984). Calibration of dentinal layers in seven captive Hawaiian spinner dolphins, Stenella longirostris, based on tetracycline labeling. Fisheries Bulletin 82(1): 207-225.

Myrick, A. C., Yochem, P. K. and L. H. Cornell. (1988). Toward calibrating dentinal layers in captive killer whales by use of tetracycline labels. Rit Fiskideildar 11: 285-296.

Nemoto, T., Okiyama, M. and M. Takahashi. (1985). Aspects of the roles of squid in food chains of marine Antarctic ecosystems. In WR Seigfried, PR Condy and RM Laws (eds.). Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin Heidelberg, pp 415-420.

Nesis, K.N. (1972). Oceanic cephalopods of the Peru current: horizontal and vertical distribution. Oceanology 12(3): 426-437.

Nesis, K.N. (1987). Cephalopods of the world. Squids, cuttlefishes, octopuses and allies. T.F.H. Publications, Inc., Ltd., Neptune City. 351pp

Nicol, D. J. (1987). A review and update of the Tasmanian cetacean stranding record to the end of February 1986. Centre for Environmental Studies Working Paper No. 21, University of Tasmania, Hobart. 93+viiipp.

Nishiwaki, M., T. Hibiya, and S. Ohsumi. (1958). Age study of sperm whale based on reading of tooth laminations. Scientific Report of the Whales Research Institute 13: 135-154+Pl I-II.

Nishiwaki, M., Ohsumi, S. and Y. Maeda. (1963). Change of form in the sperm whale accompanied with growth. Scientific Reports of the Whales Research Institute, Tokyo 17: 1-14.

Norris, K. S. (1961). Standardized methods for measuring and recording data on the smaller cetaceans. Journal of Mammalogy 42(4): 471-476.

Norris, K. S. and G. W. Harvey. (1972). A theory for the function of the spermaceti organ of the sperm whale (*Physeter catadon*). Pages 397-417 in S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs and R. E. Belleville (eds.). Animal orientation and navigation. NASA Special Publication No. 262.

Oftedal, O. T. (1997). Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. Journal of Mammary Gland Biology and Neoplasia 2(3): 205-230.

Ohsumi, S. (1965). Reproduction of the sperm whale in the north-west Pacific. Reports of the Whales Research Institute 19: 1-35.

Ohsumi, S. (1966). Sexual segregation of the sperm whale in the North Pacific. Scientific Reports of the Whales Research Institute 20: 1-16.

Ohsumi, S. (1971). Some investigations on the school structure of sperm whale. Scientific Reports of the Whales Research Institute 23: 1-25.

Ohsumi, S. (1977). Age determination and growth of Cetacea. Honyu-Kagaku 34(3): 54-63.

Ohsumi, S. (1980). Catches of sperm whales by modern whaling in the North Pacific. Reports of the International Whaling Commission (special issue 2): 11-18.

Ohsumi, S., Kasuya, T., and M. Nishiwaki. (1963). Accumulation rate of dentinal growth layers in the maxillary tooth of the sperm whale. Scientific Reports of the Whales Research Institute 17: 15-35.

Olesiuk, P. F., Bigg, M. A. and G. M. Ellis. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports of the International Whaling Commission (Special Issue 12): 209-243.

Papastavrou, V., Smith, S. C. and H. Whitehead. (1989). Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Canadian Journal of Zoology 67: 839-846.

Pascoe, P. L., Mickiewicz, M. C. and H. P. Castello. (1990). Cephalopod remains from the stomach of a sperm whale stranded off Patagonia. Marine Biology 104: 1-4.

Perrin, W. F., Coe, J. M. and J. R. Zweifel. (1976). Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fishery Bulletin 74(2): 229-269.

Perrin, W. F., Holts, D. B. and R. B. Miller. (1977). Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fishery Bulletin 75(4): 725-750.

Perrin, W. F. and A. C. Myrick (eds.). (1980). Report of the International Whaling Commission (Special Issue 3). Age determination of toothed whales and sirenians. International Whaling Commission, Cambridge, UK. 229pp.

Piatkowski U. and W. Hagen. (1994). Distribution and lipid composition of early life stages of the cranchiid squid *Galiteuthis glacialis* (Chun) in the Weddell Sea, Antarctica. Antarctic Science 6(2): 235-239.

Pierce, G. J. and P. R. Boyle (1991). A review of methods for diet analysis in piscivorous marine mammals. Oceanography and Marine Biology Annual Reviews 29: 409-486.

Pierce, K. V. and H. Kajimura. (1980). Acid etching and highlighting for defining growth layers in cetacean teeth. Report of the International Whaling Commission (special issue 3): 99-104.

Pond, C. M. (1984). Physiological and ecological importance of energy storage in the evolution of lactation: evidence for a common pattern of anatomical organisation of adipose tissue in mammals. Symposia of the Zoological Society of London 51: 1-32.

Quellar, D. C. and K. F. Goodnight. (1989). Estimation of genetic relatedness using alozyme data. Evolution 43: 258-275.

Read, A. J. (1990a). Estimation of body condition in harbour porpoises, *Phocoena phocoena.* Canadian Journal of Zoology 68 :1962-1966.

Read, A. J. (1990b). Age at sexual maturity and pregnancy rates of harbour porpoises, P*hocoena phocoena*, from the Bay of Fundy. Canadian Journal of Fisheries and Aquatic Sciences 47: 561-565.

Read, A. J. and A. A. Hohn. (1995). Life in the fast lane: the life history of harbour porpoises from the Gulf of Maine. Marine Mammal Science 11(4): 423-440.

Reijnders, P. J. H. (1986). Perspectives for studies of pollution in cetaceans. Marine Pollution Bulletin 17(2): 58-59.

Reijnders, P.J.H. (1994). Toxicokinetics of chlorobiphenyls and associated physiological responses in marine mammals with particular reference to their potential for ecotoxicological risk assessment. The Science of the Total Environment 154: 229-236.

Reijnders, P.J.H. and E.M. de Ruiter-Dijkman. (1995). Toxicological and epidemiological significance of pollutants in marine mammals. Pages 575-587 *in* A.S. Blix, L. Walløe, and Ø. Ulltang (eds). Whales, seals, fish and man. Elsevier Science, B. V., Amsterdam..

Reilly, S. B., Hohn, A. A., A. C. Myrick. (1983). Precision of age determination of northern offshore spotted dolphins. NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-35. Southwest Fisheries Center, National Marine Fisheries Service, California. 27+iv pp.

Reznick, D., Bryant, M. J. and F. Bashey. 2002. *r*-and *K*-selection revisited: the role of population regulation in life-history evolution. Ecology 83(6): 1509-1520.

Rice, D. W. (1989). Sperm whale *Physeter macrocephalus* Linnaeus, 1758. Pages 177-233 *in* S. H. Ridgeway and R. Harrison (eds.). Handbook of marine mammals, Volume 4: river dolphins and the larger toothed whales. Academic Press, San Diego.

Rice, D. W., A. A. Wolman, B. R. Mate and J. T. Harvey. (1986). A mass stranding of sperm whales in Oregon: sex and age composition of the school. Marine Mammal Science 2(1): 64-69.

Richard, K. R., M. C. Dillon, H. Whitehead and J. M. Wright. (1996). Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences, USA 93: 8792-8795.

Robison, B. H. (1989). Depth of occurrence and partial chemical composition of a giant squid, *Architeuthis* off Southern California. The Veliger 32(1): 39-42.

Robson, F. D. and P. J. H. van Bree. (1971). Some remarks on a mass stranding of sperm whales, *Physeter macrocephalus* Linnaeus, 1758, near Gisborne, New Zealand, on March 18, 1970. Sonderdruck aus zeitschrift fur Sangetierkunde 36(1): 55-60.

Rodhouse, P. G. (1989). Squid. The Southern Ocean's unknown quantity. Sea Frontiers July-August: 206-211.

Rodhouse, P. G. and M. R. Clarke. (1985). Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. Vie Milleu 35(3/4): 223-230.

Rodhouse, P. G. and C. C. Lu. (1998). *Chiroteuthis veryani* from the Atlantic sector of the Southern Ocean (Cephalopoda: Chiroteuthidae). South African Journal of Marine Science 20: 311-322.

Rodhouse, P. G. and U. Piatkowski. (1995). Fine-scale distribution of juvenile cephalopods in the Scotia Sea and adaptive allometry of the brachial crown. Marine Biology 124: 111-117.

Rodhouse, P. G., Prince, P. A., Clarke, M. R. and A. W. A. Murray. (1990). Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. Marine Biology 104: 353-362.

Rodhouse, P. G., Symon, C. and E. M. C. Hatfield. (1992). Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Marine Ecology Progress Series 89: 183-195.

Roe, H. S. J. (1969). The food and feeding habits of the sperm whales (*Physeter catadon* L.) taken off the west coast of Iceland. Journal of the Council for the International Exploration of the Sea 33(1): 93-102.

Roff, D. A. (1992). The evolution of life histories. Chapman and Hall, New York. 535+xii pp.

Roper, C. F. E., McSweeney, M. J. and C. E. Nauen. (1984). FAO Species Catalogue 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Species Synopsis 125(3). 277 pp.

Roper, C. F. E. and R. E. Young. (1975). Vertical distribution of pelagic cephalopods. Smithsonian Contributions to Zoology 209: 1-51.

Ross G. J. B. (1979). The smaller cetaceans of the southeast coast of southern Africa. PhD thesis, University of California, Los Angeles. 160 pp.

Ross, P., R. de Swart, R. Addison, H. van Loveren, J. Vos and A. Osterhaus. (1996). Contaminant-induced immunotoxicity in harbour seals: wildlife at risk? Toxicology 112: 157-169.

Ross, P.S., G.M. Ellis, M.G. Ikonomou, L.G. Barrett-Lennard and R.F. Addison. (2000). High PCB concentrations in free-ranging Pacific killer whales, *Orcinus orca*: effects of age, sex and dietary preference. Marine Pollution Bulletin 40: 504-515.

Santos, M. B., Pierce, G. J., Boyle, P. R., Reid, R. J., Ross, H. M., Patterson, I. A. P., Kinze, C. C., Tougaard, S., Lick, R., Piatowski, U. and V. Hernández-García. (1999). Stomach contents of sperm whales Physeter macrocephalus stranded in the North Sea 1990-1996. Marine Ecology Progress Series 183: 281-294.

Schantz, M. M., Koster, B. J. Wise, S. A. and P. R. Becker. (1993). Determination of PCBs and chlorinated hydrocarbons in marine mammal tissues. The Science of the Total Environment 139/140: 323-345.

Scheffer, V. B. and A. C. Myrick. (1980). A review of studies to 1970 of growth layers in the teeth of marine mammals. Report of the International Whaling Commission (special issue) 3: 51-64.

Simmonds, M. P. and S. J. Mayer. (1997). An evaluation of environmental and other factors in some recent marine mammal mortalities in Europe: implications for conservation and management. Environmental Reviews 5: 89-98.

Simonich, S. L. and R. A., Hites. (1995). Global distribution of persistent organochlorine compounds. Science 269: 1851-1854.

Skaare, J.U., Bernhoft, ., A., Derocher, A., Gabrielsen, G. W., Goksøyr, A., Henriksen, E., Larsen, H. J., Lie, E. and Ø. Wiig. (2000). Organochlorines in top predators at Svalbard - occurrence, levels and effects. Toxicology Letters 112-113: 103-109.

Slijper, E. J. (1948). On the thickness of the layer of blubber in Antarctic blue and fin whales. I. Proceedings of the Koninklijke Nederlandsche Akademie van Wetenschappen 51(8): 1033-1045.

Smith, S. C. (1992). Sperm whales and mesopelagic cephalopods in the waters of the Galapagos Islands, Ecuador. MSc thesis. Dalhousie University, Halifax. 66 pp.

Smith, S. C. and H. Whitehead. (2000). The diet of Galápagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. Marine Mammal Science 16(2): 315-325.

St. Aubin, D. J. and J. R. Geraci. (1979). Strandings: a rare look into the biology of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*. Pages 190-206 *in* J. R. Geraci and D. J. St. Aubin (eds.). Biology of marine mammals: insights through strandings. Final report to U.S. Marine Mammal Commission, MM7AC020. National Technical Information Service, U.S. Department of Commerce, Springfield, VA.

Stearns, S. C. (1992). The Evolution of life histories. Oxford University Press, Oxford. 249+xii pp.

Steinhagen-Schneider, G. (1986). Cadmium and copper levels in seals, penguins and skuas from the Weddell Sea in 1982/1983. Polar Biology 5: 139-143.

Stephenson, A. B. (1975). Sperm whales stranded at Muriwai beach, New Zealand. New Zealand Journal of Marine and Freshwater Research 9(3): 299-304.

Stewart, R. E. A. and D. M. Lavigne. (1984). Energy transfer and female condition in nusing harp seals *Phoca groenlandica*. Holarctic Ecology 7: 182-194.

Stewart, R. E. A., Stewart, B. E., Stirling, I. and E. Street. (1996). Counts of growth layer groups in cementum and dentine in ringed seals (*Phoca hispida*). Marine Mammal Science 12(3): 383-401.

Subramanian, An., Tanabe, S., Tatsukawa, R., Saito, S. and N. Miyazaki. (1987). Reduction in the testosterone levels by PCBs and DDE in Dall's porpoises of northwestern North Pacific. Marine Pollution Bulletin 18(12): 643-646.

Suydam, R. S. (1999). Age, growth and reproduction of beluga whales from the eastern Chakchi Sea, Alaska. Paper SC/51/SM40 presented to the Scientific Committee of the International Whaling Commission. 16pp.

Tanabe, S., Iwata, H. and R. Tatsukawa. (1994). Global contamination by persistent organochlorines and the ecotoxicological impact on marine mammals. The Science of the Total Environment 154: 163-177.

Tanabe, S., Mori, T. and R. Tatsukawa. (1983). Global pollution of marine mammals by PCBs, DDTs and HCHs (BHCs). Chemosphere 12(9): 1269-1275.

Tanabe, S., Tanaka, H. Maruyama, K. and R. Tatsukawa. (1980). Elimination of chlorinated hydrocarbons from mother striped dolphins (*Stenella coeruleoalba*) through parturition and lactation. Pages 115-121 *in* T. Fujiyama (ed.). Studies on the levels of organochlorine compounds and heavy metals in the marine organisms. University of the Ryukus, Okinawa.

Tanabe, S., Tatsukawa, R., Tanaka, H., Maruyama, K., Miyazaki, N. and T. Fujiyama. (1981). Distribution and total burdens of chlorinated hydrocarbons in bodies of striped dolphins (*Stenella coeruleoalba*). Agricultural and Biological Chemistry 45(11): 2569-2578.

Tanabe, S., S. Watanabe, H. Kan and R. Tatsukawa. (1988). Capacity and mode of PCB metabolism in small cetaceans. Marine Mammal Science 4: 103-124.

Taruski, A. G., Olney, C. E. and H. E. Winn. (1975). Chlorinated hydrocarbons in cetaceans. Journal of the Fisheries Research Board of Canada 32: 2205-2209.

Taylor, B. (1999). Refining the definition of stocks: a discussion paper. Paper IWC/51/RMP23 presented to the Scientific Committee of the International Whaling Commission. 8pp.

Taylor, B. L. and A. E. Dizon. (1999). First policy then science: why a management unit based solely on genetic criteria cannot work. Molecular Ecology 8: 511-516.

The Tree of Life Web Project. (2001). http://www.tolweb.org/tree/.

Tilbury, K.L., Adams, N. G., Krone, C. A., Meador, J. P., Early, G. and U. Varanasi. (1999). Organochlorines in stranded pilot whales (*Globicephala melaena*) from the coast of Massachusetts. Archives of Environmental Contamination and Toxicology 37: 125-134.

Townsend, C. H. (1935). The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19(1-2): 1-52.

Trillmich, F., Ono, K. A., Costa, D. A., DeLong, R. L., Feldkamp, S. D., Francis, J. M., Gentry, R. L., Heath, C. B., LeBoeuf, B. J., Maljuf, P. and A. E. York. (1991). The effects of El Niño on pinniped populations in the eastern Pacific. Pages 247-270 *in* F. Trillmich and K. A. Ono (eds.). Pinnipeds and El Niño. Responses to environmental stress. Springer-Verlag, Berlin.

Trites, A. W. (1991). Fetal growth of northern fur seals: life history strategies and sources of variation. Canadian Journal of Zoology 65: 1091-1099.

Trites, A. W. and M. A. Bigg. (1992). Changes in the growth of northern fur seals from 1958 to 1974: density effects or changes in the ecosystem? Fisheries Oceanography 1: 127-136.

Van den Berg, M., L. Birnbaum, A.T.C. Bosveld, B. Brunström, P. Cook, M. Feeley, J.P. Giesy, A. Hanberg, R. Hasegawa, S.W. Kennedy, T. Kubiak, J.C. Larsen, F.X.R. van Leeuwen, A.K.D. Liem, C. Nolt, R.E. Peterson, L. Poellinger, S. Safe, D. Screnk and D. Tillit. (1998). Toxic equivalency factors (TEFs) for PCBs, PCDDs, PCDFs for humans and wildlife. Environmental Health Perspectives 106: 775-792.

Van Dyk, L. P., Wiese, I. H. and E. C. Mullen. (1982). Management and determination of pesticide residues in South Africa. Residue Reviews 82: 37-124.

von Bertalanffy, L. (1938). A quantitative theory of organic growth. Human Biology 10(2): 181-213.

Voss, N. A. (1969). A monograph of the Cephalopoda of the North Atlantic. The family Histioteuthidae. Bulletin of Marine Science 19(4): 713-867.

Voss, N. A. (1985). Systematics, biology and biogeography of the cranchiid cephalopod genus *Teuthowenia* (Oegopsida). Bulletin of Marine Science 36(1): 1-85.

Wahlberg, M. (2002). The acoustic behaviour of diving sperm whales observed with a hydrophone array. The Journal of Experimental Marine Biology and Ecology 281: 53-62.

Wania, F and D. Mackay. (1995). A global distribution model for persistent organic pollutants. The Science of the Total Environment 160/161, 211-232.

Waring, G. T., Fairfield, C. P., Ruhsam, C. M. and M. Sano. (1993). Sperm whales associated with Gulf Stream features off the north-eastern USA shelf. Fisheries Oceanography 2(2): 101-105.

Waring, G. T., Hamzaki, T., Sheehan, D., Wood, G. and S. Baker. (2001). Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the northeast U.S. Marine Mammal Science 17(4): 703-717.

Warneke, R. M. (1997). Tasmanian whale rescue plan. An action plan for cetacean contingencies including an overview of strandings in Tasmania, 1825-1995 and synopses of the species involved. Parks and Wildlife Service, Department of Environment and Land Management, Tasmania. 177+vii pp

Waters, S. and H. Whitehead. (1990). Population and growth parameters of Galápagos sperm whales estimated from length distributions. Report of the International Whaling Commission 40: 225-235.

Watkins, W. A., Daher, M. A., DiMarzio, N. A., Samuels, A., Wartzok, D., Frisrup, K. M., Gannon, D. P., Howey, P. W. and R. R. Maiefski. (1999). Sperm whale surface activity from tracking by radio and satellite tags. Marine Mammal Science 15(4): 1158-1180

Watkins, W. A., Daher, M. A., Fristrup, K. M. and T. J. Howald. (1993). Sperm whales tagged with transponders and tracked underwater by sonar. Marine Mammal Science 9(1): 55-67.

Watkins, W. A., Moore, K. E. and P. Tyack. (1985). Investigations of sperm whale acoustic behaviours in the southeast Carribean. Cetology 49: 1-15.

Watkins, W. A. and W. E. Schevill. (1977). Spatial distribution of *Physeter catadon* (sperm whales) underwater. Deep-Sea Research 24: 693-699.

Wells, D. E., McKenzie, C. and H. M. Ross. (1997). Patterns of organic contaminants in marine mammals with reference to sperm whale strandings. Bulletin de L'Institut Royal des Sciences Naturelles de Belgique 67 - supplement: 91-104.

Wells, R. S., and M. D. Scott. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. Report of the International Whaling Commission Special Issue 12: 407-417.

Whitehead, H. (1989). Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Isalnds. Canadian Journal of Zoology 67: 2131-2139.

Whitehead, H. (1990). Assessing sperm whale populations using natural markings: recent progress. Reports of the International Whaling Commission (Special Issue 12): 377-382.

Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. Marine Ecology Progress Series 242: 295-304.

Whitehead, H., Brennan, S., and D. Grover. (1992). Distribution and beahviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70: 912-918.

Whitehead, H. and B. Kahn. (1992). Temporal and geographic variation in the social structure of female sperm whales. Canadian Journal of Zoology 70: 2145-2149.

Whitehead, H., Waters, S. and T. Lyrholm. (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behavioural Ecology and Sociobiology 29: 385-389.

Whitehead, H. and L. Weilgart. (1991). Patterns of visually observable behaviour and vocalisations in groups of female sperm whales. Behaviour 118: 275-296.

Whitehead, H. and L. Weilgart. (2000). The sperm whale: social females and roving males. Pages 154-172 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead (eds.). Cetacean Societies: field studies of dolphins and whales. The University of Chicago Press, Chicago.

Wolff, G. A. (1984). Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. NOAA Technical Report NMFS 17. U.S. Department of Commerce. 50+ivpp.

Wolman, A. A. and A. J. Wilson. (1970). Occurrence of pesticides in whales. Pesticides Monitoring Journal 4(1): 8-10.

Woodd, A. M. (1999). A demographic model to predict future growth of the Addo elephant population. Koedoe 42/1: 97-100.

Worthy, G. A. J. and E. F. Edwards. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). Physiological Zoology 63(2): 432-442.

Zeh, J. E., George, J. C. and R. Suydam. (1995). Population size and rate of increase, 1978-1993, of bowhead whales, *Balaena mysticetus*. Reports of the International Whaling Commission 45: 339-344.

APPENDIX

The following publications are derived or partly-derived from research associated with this project. Reprints or manuscripts of these are included in the following pages.

Evans, K. (In Press). Pollution and marine mammals in the Southern Hemisphere. Present or potential threat? In N. J. Gales, M. A. Hindell and R. Kirkwood (eds.). Marine mammals. Fisheries, tourism and management issues. CSIRO Publishing, Melbourne.

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. Behavioural and Brain Sciences 24(2): 346-347.

Mesnick, S. L., Evans, K., Taylor, B. L., Hyde, J., Escorza-Treviño, S., and A. E. Dizon. (2003). Sperm whale social structure: why it takes a village to raise a child. Pages 170-174 in B. M. D. Wall and P. L. Tyack (eds.). Animal social complexity. Intelligence, culture and individualized societies. Harvard University Press, New York.

POLLUTION AND MARINE MAMMALS IN THE SOUTHERN HEMISPHERE: POTENTIAL OR PRESENT THREAT?

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Note: full appendices associated with this chapter can be accessed at: http://www.zoo.utas.edu.au/awru/ or by contacting the author at the address listed above.

Table One: Mean concentration ± SD (range, n) of DDT and its metabolites, ΣDDT and the ratios %DDE/ΣDDT and %ΣDDT/ΣPCB in the blubber of marine mammals in the five regions of the Southern Hemisphere.

Region	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
Antarctic/ sub-Antarctic	0.1±0.2 (0.0-0.7; **52**)	0.1±0.2 (0.01-1.4; **90**)	0.03±0.2 (0.0-0.1; **32**)	0.3±0.4 (0.01-2.4; **146**)	0.2±0.5 ($5.6x10^{-8}$-3.0; **193**)	53.0±13.0 (0.0-84.4; **136**)	387.0±616.4 (9.8-2293.3; **145**)
South America	2.9±3.2 (0.002-10.0; **20**)	2.1±1.9 (0.05-6.4; **20**)	1.0±1.2 (0.01-4.0; **19**)	7.8±9.6 (0.05-30.9; **24**)	3.7±3.8 (0.2-18.0; **21**)	39.3±20.4 (8.0-88.4; **20**)	210.1±230.4 (22.11-956.6; **21**)
South Africa	0.6±1.3 (0.0-8.5; **112**)	2.3±5.3 (0.0-32.0; **112**)	0.1±0.4 (0.0-3.7; **112**)	6.6±12.1 (0.0-85.7; **295**)	5.3±8.9 (0.0-67.2; **292**)	57.2±33.3 (0.0-100.0; **112**)	161.9±186.1 (0.01-1217.65; **290**)
Australia	1.2±2.8 (0.03-19.2; **70**	1.3±1.8 (0.03-11.4; **68**)	0.2±0.2 (0.01-1.1; **55**)	2.6±4.1 (0.1-19.6; **69**)	1.5±3.0 (0.01-19.6; **76**)	59.3±18.9 (7.2-98.8; **64**)	420.4±751.8 (45.3-5375.0; **55**)
New Zealand/ South Pacific	0.5±0.8 (0.8-1.8; **4**)	4.0±2.4 (1.6-7.2; **4**)	0.4±0.2 (0.3-0.7; **4**)	7.2±3.1 (3.6-11.2; **5**)	0.5±0.8 (0.01-5.2; **79**)	58.0±14.5 (43.7-75.3; **4**)	583.3±426.9 (114.8-1168.0; **5**)

All values μg g^{-1} wet weight.
Samples sizes are minimums as not all references stated sample sizes.

Table Two: Mean concentration ± SD (range, n) of DDT and its metabolites, ΣDDT and the ratios %DDE/ΣDDT and %ΣDDT/ΣPCB in the blubber of marine mammal taxonomic/ecotype groups in the five regions of the Southern Hemisphere.

Region/Group	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
Pinnipeds							
Antarctic/ sub-Antarctic	0.02±0.02 (0.001-0.1; **29**)	0.1±0.02 (0.03-0.1; **30**)	0.1±0.01 (0.003-0.1; **20**)	0.1±0.1 (0.01-0.2; **34**)	0.1±0.1 ($5.6x10^{-8}$-0.8; **44**)	51.6±16.7 (31.5-100.0; **30**)	689.7±762.2 (14.1-2293.3; **4**)
South Africa	0.6±1.9 (0.0-7.9; **21**)	3.0±6.1 (0.0-23.0; **21**)	0.004±0.01 (0.0-0.1; **21**)	3.7±7.9 (0.0-30.9; **21**)	1.4±4.4 (0.0-20.2; **21**)	55.3±32.2 (28.6-100.0; **21**)	421.7±221.5 (44.8-1040.2; **18**)
Australia	1.3±1.8 (0.1-6.8; **12**)	2.4±3.1 (0.1-11.4; **12**)	0.01±0.01 (0.0-0.03; **11**)	3.8±3.6 (0.5-12.1; **12**)	0.7±1.0 (0.1-3.9; **12**)	59.5±26.0 (7.2-95.8; **12**)	735.5±405.9 (106.2-1385.9; **12**)
Mysticetes							
Antarctic/ sub-Antarctic	0.02±0.01 (0.01-0.1; **12**)	0.1±0.04 (0.01-0.2; **49**)	0.01±0.004 (0.001-0.02; **12**)	0.1±0.1 (0.02-0.2; **101**)	0.1±0.1 (0.0-0.9; **138**)	64.8±7.3 (54.2-77.0; **12**)	93.2±69.5 (9.8-289.5; **101**)
South America	0.1±0.1 (0.002-0.1; **3**)	0.2±0.4 (0.1-0.6; **3**)	0.1±0.2 (0.01-0.3; **3**)	0.4±0.7 (0.1-1.0; **3**)	–	60.3±27.8 (32.9-88.4; **3**)	–
South Africa	0.1±0.2 (0.04-0.8; **36**)	0.04±0.1 (0.02-0.3; **36**)	0.04±0.01 (0.03-0.1; **36**)	0.2±0.2 (0.01-0.8; **40**)	0.5±0.1 (0.01-0.5; **37**)	43.6±35.3 (3.9-100.0; **36**)	59.29±132.0 (4.0-800.0; **4**)
Australia	0.2±0.3 (0.03-0.5; **3**)	0.2±0.3 (0.03-0.5; **3**)	0.1±0.1 (0.03-0.1; **2**)	0.4±0.6 (0.1-1.1; **3**)	0.01 (0.01; **1**)	42.9±8.6 (33.3-50.0; **3**)	–
Coastal odontocetes							
Antarctic/ sub-Antarctic	0.3±0.2 (0.1-0.7; **11**)	0.5±0.4 (0.1-1.4; **11**)	–	1.0±0.6 (0.2-2.4; **11**)	1.3±0.8 (0.4-3.0; **11**)	47.5±8.9 (33.0-61.1; **11**)	71.5±23.8 (38.2-102.4; **11**)
South America	3.6±3.3 (0.1-10.0; **16**)	2.6±1.8 (0.1-6.40; **16**)	1.2±1.2 (0.02-4.0; **16**)	11.3±10.1 (0.2-30.9; **16**)	4.4±4.0 (0.5-18.0; **16**)	34.8±17.6 (8.0-68.1; **16**)	258.9±244.6 (42.3-965.6; **16**)
South Africa	1.1±1.6 (0.0-5.0; **8**)	6.7±8.2 (0.3-23.7; **8**)	0.3±0.5 (0.0-1.2; **8**)	11.5±15.9 (0.04-85.7; **129**)	9.8±10.8 (0.0-67.2; **129**)	70.1±26.1 (28.7-100.0; **8**)	148.73±1840.4 (0.9-1217.7; **125**)
Australia	19.2 (19.2; **1**)	0.7±0.5 (0.4-1.1; **2**)	–	1.3±1.6 (0.2-2.4; **2**)	4.2±6.3 (0.1-19.6; **13**)	–	–
Pelagic odontocetes							
South Africa	0.7±1.5 (0.0-8.5; **47**)	2.9±5.7 (0.0-32.0; **47**)	0.2±0.6 (0.0-3.7; **47**)	3.6±5.7 (0.0-33.8; **105**)	2.3±5.3 (0.0-33.8; **105**)	66.3±30.3 (0.02-100.0; **47**)	171.7±145.1 (29.5-794.4; **171**)
Australia	0.9±1.7 (0.1-10.0; **48**)	0.9±0.9 (0.03-5.4; **48**)	0.2±0.2 (0.02-1.1; **39**)	2.5±4.4 (0.0-28.4; **41**)	0.8±0.6 (0.03-3.3; **42**)	58.1±15.1 (21.6-87.5; **46**)	344.4±833.3 (45.3-52.8; **40**)

Table Two continued.

Region/Group	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
New Zealand/ South Pacific	1.1±0.5 (0.8-1.8; **4**)	4.0±2.4 (1.6-7.2; **4**)	0.4±0.2 (0.3-0.7; **4**)	7.2±3.1 (3.7-11.2; **5**)	0.5±0.8 (0.03-5.2; **76**)	58.0±14.5 (43.7-75.3; **4**)	583.3±426.9 (114.8-1168.0; **5**)
Sirenians							
Australia	0.05 (0.05; **3**)	4.0±3.7 (0.9-8.0; **3**)	0.05 (0.05; **3**)	4.1±3.6 (1.0-8.1; **3**)	2.2±1.1 (0.9-3.1; **3**)	95.2±4.6 (90.0-98.8; **3**)	1740.6±120.2 (101.0-312.7; **3**)

All values μg g^{-1} wet weight.
Samples sizes are minimums as not all references stated sample sizes.

Table Three: Mean concentration ± SD (range, n) of DDT and its metabolites, ΣDDT, ΣPCB and the ratios %DDE/ΣDDT and %ΣDDT/ΣPCB in the blubber of various age and sex groups of marine mammal species throughout the Southern Hemisphere.

Species	Age/ Sex[1]	Region[2]	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
Fur seals	AF	SAF	0.1±0.1 (0.0-0.2; **3**)	4.5±3.9 (2.2-9.1; **3**)	0.0 (0.0; **3**)	4.6±3.9 (2.3-9.1; **3**)	7.1±11.4 (0.4-20.2; **3**)	96.4±3.5 (93.1-100.0; **3**)	352.6±282.5 (44.8-600.0; **3**)
		AUS	0.5±0.2 (0.2-0.7; **4**)	1.4±1.4 (0.2-3.4; **4**)	0.01±0.01 (0.01-0.02; **4**)	1.9±1.5 (0.5-4.1; **4**)	0.4±0.2 (0.1-0.5; **4**)	65.5±14.6 (48.5-83.0; **4**)	617.6±260.5 (283.5-873.4; **4**)
	JM	SAF	0.0 (0.0; **1**)	0.5 (0.5; **1**)	0.1 (0.1; **1**)	0.5 (0.5; **1**)	0.0 (0.0; **1**)	87.3 (87.3; **1**)	–
		AUS	1.2±0.3 (0.6-1.6; **5**)	3.9±4.4 (1.0-11.4; **5**)	0.02±0.01 (0.01-0.03; **5**)	5.1±4.2 (2.1-12.1; **5**)	1.0±1.6 (0.2-3.9; **5**)	63.7±19.9 (46.6-94.7; **5**)	915.4±404.5 (310.9-1385.9; **5**)
	AM	SAF	0.7±2.1 (0.0-7.9; **14**)	2.4±6.6 (0.0-23.0; **14**)	0.0 (0.0; **14**)	3.1±8.6 (0.0-30.9; **14**)	0.5±1.2 (0.0-3.5; **14**)	36.0±19.2 (28.6-87.2; **14**)	392.4±143.0 (350.0-886.2; **14**)
		AUS	3.6±4.5 (0.5-6.8; **2**)	1.5±1.9 (0.1- 2.9; **2**)	0.01 (0.01; **2**)	5.7±5.6 (1.7-9.7; **2**)	0.6±0.3 (0.4-0.8; **2**)	18.4±15.8 (7.22-29.6; **2**)	836.1±565.9 (436.0 -1236.2; **2**)
Minke whales	JF	ASA	–	0.04±0.02 (0.03-0.1; **5**)	–	–	0.01±0.004 (0.004-0.01; **5**)	–	–
		SAF	0.2±0.2 (0.04-0.5; **7**)	0.1±0.1 (0.02-0.3; **7**)	0.04±0.01 (0.04-0.1; **7**)	0.2±0.3 (0.03-0.8; **8**)	0.4±0.2 (0.01-0.5; **7**)	45.2±39.0 (11.1-100.0; **7**)	151.7±291.1 (6.0-800.0; **7**)
	AF	ASA	–	0.04±0.02 (0.01-0.1; **9**)	–	–	0.01±0.004 (0.01-0.1; **9**)	–	–
		SAF	0.1±0.1 (0.04-0.2; **4**)	0.02±0.0 (0.02; **4**)	0.04±0.0 (0.04; **4**)	0.1±0.1 (0.02-0.2; **4**)	0.5±0.0 (0.5; **4**)	41.3±40.1 (11.8-100.0; **4**)	19.3±15.0 (4.0-34.0; **3**)
	JM	ASA	–	0.1±0.02 (0.03-0.1; **7**)	–	–	0.01±0.002 (0.01-0.01; **7**)	–	–
		SAF	0.2±0.4 (0.04-0.8; **4**)	0.2±0.4 (0.04-0.8; **4**)	0.04 (0.04; **4**)	0.2±0.4 (0.02-0.8; **4**)	0.5 (0.5; **4**)	56.0±51.3 (3.8-100.0; **4**)	46.5±73.3 (4.0-156.0; **4**)
	AM	ASA	–	0.1±0.03 (0.04-0.1; **13**)	–	–	0.02±0.01 (0.01-0.03; **13**)	–	–
Minke whales	AM	SAF	0.1±0.1 (0.04-0.5; **11**)	0.03±0.02 (0.02-0.1; **11**)	0.05±0.02 (0.03-0.08; **11**)	0.1±0.1 (0.02-0.6; **11**)	0.5 (0.5; **10**)	31.6±26.5 (5.3-100.0; **11**)	31.0±30.6 (4.0-114.0; **10**)

Table Three continued.

Species	Age/ Sex[1]	Region[2]	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
		NZSP	–	–	–	–	0.2 (0.2; **1**)	–	–
Bottlenose dolphins	JF	SAF	0.5±0.7 (0.0-1.3; **3**)	2.0±2.9 (0.3-5.4; **3**)	0.2±0.3 (0.0-0.6; **3**)	6.2±10.3 (0.1-49.7; **21**)	8.6±10.0 (0.0-47.6; **21**)	64.0±25.1 (35.2-80.9; **3**)	70.1±40.1 (0.9-157.0; **19**)
		AUS	–	–	–	–	3.3 (3.3; **1**)	–	–
Bottlenose dolphins	AF	SAF	–	–	–	5.0±5.4 (0.04-22.9; **35**)	7.7±10.6 (0.1-43.0; **35**)	–	86.3±79.6 (13.0-321.6; **35**)
		AUS	–	–	–	–	0.9 (0.9; **1**)	–	–
	AM	SAF	–	–	–	23.2±20.8 (0.2-71.9; **34**)	14.62±13.20 (0.16-67.18; **34**)	–	200.3±213.9 (33.5-1217.6; **34**)
		AUS	–	–	–	–	5.1±6.9 (0.6-19.6; **10**)	–	–
Common dolphins	AM	SAF	–	–	–	6.1±4.0 (0.1-9.8; **8**)	3.6±2.5 (0.1-6.9; **8**)	–	164.2±78.6 (100.0-341.3; **8**)
		NZSP	–	–	–	–	0.9±0.9 (0.3, 1.5; **2**)	–	0.0 (0.0; **2**)
Striped dolphins	JM	SAF	2.9 (2.9; **1**)	2.3 (2.3; **1**)	1.2 (1.2; **1**)	3.5±3.9 (0.7, 6.3; **2**)	0.6±0.8 (0.0, 1.1; **2**)	36.4 (36.4; **1**)	66.7 (66.7; **1**)
		NZSP	1.0 (1.0; **1**)	2.8 (2.8; **1**)	0.4 (0.4; **1**)	5.7 (5.7; **1**)	5.0 (5.0; **1**)	48.8 (48.8; **1**)	114.8 (114.8; **1**)
Dusky dolphins	AM	SAF	–	–	–	5.2±4.2 (2.2, 8.2; **2**)	2.91±1.88 (1.58, 4.24; **2**)	–	166.3±37.3 (139.9-192.7; **2**)
		NZSP	–	–	–	–	1.0 (1.0; **1**)	–	–
Sperm whales	JF	SAF	0.1±0.03 (0.0, 0.1; **2**)	0.2±0.1 (0.1, 0.2; **2**)	0.04±0.0 (0.04; **2**)	0.2±0.02 (0.2, 0.2; **2**)	0.3±0.4 (0.0, 0.5; **2**)	71.4±40.4 (42.9-100.0; **2**)	46.0 (46.0; **1**)
		AUS	0.3±0.4 (0.1-0.8; **3**)	1.3±1.4 (0.3-2.9; **3**)	0.3±0.4 (0.05-0.8; **3**)	1.9±1.6 (0.5-3.7; **3**)	1.0±1.1 (0.4-2.3; **3**)	60.5±20.4 (38.2-78.1; **3**)	217.5±144.1 (107.3-380.6; **3**)

Table Three continued

Species	Age/ Sex[1]	Region[2]	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT	ΣPCB	%DDE/ΣDDT	%ΣDDT/ΣPCB
	JM	SAF	0.2±0.2	0.2±0.1	0.04±0.01	0.5±0.3	0.5±0.1	59.2±26.3	94.5±62.5
			(0.0-0.8; **12**)	(0.1-0.4; **12**)	(0.0-0.06; **12**)	(0.2-1.2; **12**)	(0.0-0.5; **12**)	(35.2-100.0; **12**)	(34.0-244.0; **11**)
		AUS	1.0±1.1	1.8±2.1	0.4±0.4	3.2±.3.6	1.3±1.2	58.9±9.2	217.4±87.9
			(0.1-2.9; **5**)	(0.2-5.4; **5**)	(0.1-1.1; **5**)	(0.3-9.4; **5**)	(0.4-3.3; **5**)	(45.0-67.6; **5**)	(72.7-289.6; **5**)

All values μg g^{-1} wet weight.
[1]Age/Sex: A: adult; J: juvenile; F: female; M: male
[2]Region: ASA: Antarctic/sub-Antarctic; SAM: South America; SAF: South Africa; AUS: Australia; NZSP: New Zealand/South Pacific

Table Four(a) and (b): Mean concentration ± SD (range) of organochlorines in the blubber of selected marine mammals from the Northern Hemisphere.

Table Four(a): Concentrations of DDTs.

Species	Area	Year	Source of sample	Sex/Age^	n	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT
Pinnipeds									
P. vitulina[1]	Schleswig-Holstein, Wadden Sea	1987	STR	JF	5				2.6±2.4 (0.4-6.6)
				JM	7				2.8±1.8 (1.1-5.2)
H. greyi[1]	Iceland	U	SS	AF	3				0.7±0.3 (0.4-1.0)
				AM	5				0.8±0.5 (0.2-1.6)
M. angustirostris[2]	Año Nuevo/Sausalito, California	U	B	JU	1				
C. ursinus[3]	St. Paul Island, Alaska	1987	U	JM	2				
C. ursinus[4]	St. Paul Island, Alaska	1972	B	AF	2	1.6±0.9 (0.9, 2.2)	2.9±1.3 (2.0, 3.8)	0.7±0.4 (0.4, 1.0)	8.1±1.1 (7.3, 8.9)
				JU	5	1.8±1.3 (0.1-3.2)	36.1±44.9 (3.3-98.0)	1.9±2.0 (0.1-4.7)	43.0±46.3 (5.3-106.4)
Mysticetes									
B. acutorostrata[5]	North Pacific	1994	W	AM	18				1.7 (0.2-2.6)
B. acutorostrata[6]	Finnmark/Barents Sea, Norway	1992	W	UF	30				1.4 (0.6-2.9)
B. borealis[7]	North Pacific	1982-85	W	UM	14	0.1±0.04	0.1±0.1	0.1±0.03	0.2±0.2
				UF	26	0.02±0.01	0.03±0.02	0.02±0.01	0.1±0.1
B. musculus[8]	St. Lawrence River, Canada	U	U	U	2				<5.0
B. physalus[9]	North Atlantic	1982-84	W	JF	41	0.1	0.2	0.1	0.7
				AF	24	0.1	0.1	0.1	0.3
				JM	20	0.1	0.2	0.1	0.7
				AM	22	0.2	0.6	0.2	1.3

Table Four(a) continued.

Species	Area	Year	Source of sample	Sex/Age	n	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT
E. glacialis[10]	Bay of Fundy/ Browns-Baccaro Banks	1989	B	JM	3	0.1±0.1 (0.0-0.2)	0.04±0.01 (0.03-0.1)	0.03±0.02 (0.0-0.04)	0.1±0.04 (0.03-0.1)
				AF	6	0.01±0.03 (0.0-0.1)	0.03±0.03 (0.0-0.1)	0.003±0.01 (0.0-0.02)	0.04±0.02 (0.02-0.1)
				AM	6	0.04±0.1 (0.0-0.1)	0.2±0.2 (0.02-0.4)	0.01±0.02 (0.0-0.1)	0.2±0.2 (0.02-0.5)
Coastal Odontocetes									
P. gangetica[13]	Ganges River, Patna	1988-92	BY	JM	2				6.9±3.1 (4.7, 9.1)
				JF	1				12.0
				AF	1				13.0
P. phocoena[14]				AF	2				29.5±16.3 (18.0, 41.0)
				JM	15				55.5±27.0 (25.0-120.0)
				AM	8				87.5±50.0 (34.0-180.0)
T. truncatus[15]	Gulf of Mexico	1990	STR	JF&JM	5	1.4 (0.8-2.3)	0.01 (0.01-0.02)		
				AF	5	0.01 (ND-0.02)	0.004 (0.001-0.01)		
				AM	9	0.9 (0.2-2.0)	0.04 (0.02-0.1)		
S. chinensis[16]	Hong Kong	1993-97	STR/BY/W	AM	7				
Sirenians									
T. manatus latirostris[11]	Florida	1990-93	STR	JM	1				
T. manatus latirostris[12]	Florida	1977-81	STR	U	26				0.2±0.1 (0.1-0.3)
Pelagic Odontocetes									
D. delphis[17]	Southern California	1968-76	STR	AF	2	18.7±2.5 (16.0-21.0)	680.0±298.2 (360.0-950.0)	33.0±15.7 (22.0-51.0)	
				AM	10	20.8±7.0 (13.0-36.0)	925.0±418.0 (500.0-1700.0)	39.5±23.5 (19.0-98.0)	

Table Four(a) continued.

Species	Area	Year	Source of sample	Sex/Age^	n	*p, p'*-DDT	*p, p'*-DDE	*p, p'*-DDD	ΣDDT
S. coeruleoalba[17]	Japan	1968-76	STR	AF	4	2.3±1.9 (0.6-4.6)	4.9±4.9 (0.64-10.0)	0.7±0.7 (ND-1.4)	
				AM	1	4.4	12.0	0.8	
L. acutus[7]	Faroe Islands	1987	W	UM	8	2.8±1.2	12.6±6.4	2.7±1.1	18.0±8.3
				UF	5	2.0±1.6	8.6±8.9	2.0±1.7	12.5±12.1
L. borealis[16]	North Pacific	1991	STR/BY/W	AM	1				
G. griseus[18]	British Columbia	1988	STR	AM	1	0.3	4.2	0.1	5.0
G. griseus[19]	Adriatic Sea	1992	STR	JF	1				5.2
G. melas[20]	Faroe Islands	1987	W	JF	44				37.2±26.9
				AF	113				9.2±9.1
				JM	15				49.1±32.5
				AM	11				50.9±20.7
P. crassidens[18]	British Columbia	1987-89	STR	AM	2	63.6±79.8 (7.1, 120.0)	880.0±1159.7 (60.0, 1700.0)	18.7±23.1 (23.0, 35.0)	988.0±1289.8 (76.0, 1900.0)
O. orca[18]	British Columbia	1986-89	STR	AF(1), JM(5)	6	1.3	28.0	1.9	32.0
M. densirostris[21]	New Jersey	1971-75	U	JM	1	35.0	22.0	8.1	65.1
	South Carolina	1971-75	U	AM	1	15.0	19.0	4.2	38.2
Z. cavirostris[22]	Bermuda	1981	STR	AF	1	5.4	5.7	1.13	12.3
				AM	3	11.7±4.9 (8.2-17.3)	13.5±4.4 (8.5-17.0)	5.7±3.6 (3.2-9.8)	11.7±489.0 (8.2-17.3)
P. macrocephalus[21]	Anegada Passage	1971-75	U	AF	1	4.0	9.9	1.6	15.5
				AM	1	0.2	0.8	0.1	1.1
P.macrocephalus[23]	North Sea	1994-95		JM	7	1.5±0.3 (1.1-1.9)	4.1±0.7 (3.0-5.2)	0.5±0.1 (0.3-0.7)	7.0±1.3 (5.4-9.1)

Table Four(b): Concentrations of ΣPCB, ΣCHL, ΣHCH, ΣHCB, ΣHCB, Lindane and Dieldrin.

Species	Sex/Age	ΣPCB	ΣCHL	ΣHCH	ΣHCB	Lindane	Dieldrin	Comments
Pinnipeds								
P. vitulina[1]	JF	10.7±8.8 (2.0-11.3)						ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD; ΣPCB=sum of congeners 153+138/163
	JM	11.6±6.0 (4.0-18.6)						
H. greyi[1]	AF	0.7±0.4 (0.3-1.0)		0.03±0.01 (0.02-0.04)	0.04±0.04 (0.01-0.1)			ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD; ΣPCB= sum of congeners 153, 138, 180; ΣHCH=α-HCH
	AM	0.7±0.4 (0.3-1.4)		0.02±0.01 (0.01-0.03)	0.03±0.04 (0.01-0.1)			
M. angustirostris[2]	JU	3.4 (0.4-1.5)	1.3 (0.5-0.8)		0.03			ΣPCB=118+153+138+180; ΣCHL=*trans*-nonachlor+oxychlordane+heptachlor epoxide
C. ursinus[3]	JM	0.4±0.2 (0.3-0.6)	0.2±0.2 (0.1-0.3)		ND	0.01±0.02 (0.001-0.03)	0.01±0.02 (0.001-0.03)	ΣPCB=sum of 15 congeners; ΣCHL=*cis*-+*trans*-nonachlor+heptachlor epoxide
C. ursinus[4]	AF	5.8±1.5 (4.7, 6.8)					0.1±0.1 (0.1, 0.2)	ΣDDT=*o,p'*-DDT+*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD+*o,p'*-DDD; ΣPCBs=Aroclor 1254
	JU	21.9±33.5 (1.3-81.0)					0.03±0.1 (0.0-0.1)	
Mysticetes								
B. acutorostrata[5]	AM	2.3 (0.6-3.1)	0.4 (0.01-0.6)	0.3 (0.1-0.7)	0.1 (0.1-0.3)			ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD; ΣCHL=cis-chlordane+*trans*-+*cis*-nonachlor+oxychlodane; ΣHCH=α+β+γ
B. acutorostrata[6]	UF	2.0 (1.1-41)						ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD+*o,p'*-DDT+*o,p'*-DDD; ΣPCBs= sum of congeners 28, 52, 74, 99, 101, 105, 110, 114, 118, 128, 138, 153, 156, 157, 170, 180, 187, 194, 206, 209
B. borealis[7]	UM	0.3±0.2						
	UF	0.1±0.1						
B. musculus[8]	U	<5.0						Doesn't state what ΣDDT and ΣPCB composed of
B. physalus[9]	JF	0.4						
	AF	0.5						
	JM	0.4						

Table Four(b) continued

Species	Sex/Age	ΣPCB	ΣCHL	ΣHCH	ΣHCB	Lindane	Dieldrin	Comments
	AM	1.4						
E. glacialis[10]	JM	0.9±0.4 (0.6-1.4)						ΣDDT=*p,p'*-DDE+*p,p'*-DDD+p,p'-DDT; ΣPCB=Aroclor 1254; ΣCHL=*trans*-+*cis*-chlordane+*cis*-+heptachor epoxide
	AF	0.4±0.2 (0.1-0.7)						
	AM	0.7±0.7 (0.0-1.9)						
Coastal Odontocetes								
P. gangetica[13]	JM	0.4±0.04 (0.4, 0.4)	0.03±0.03 (0.01, 0.1)	0.3±0.2 (0.2, 0.5)	0.004±0.01 (0.003, 0.01)		0.1±0.001 (0.1, 0.1)	ΣDDT=*o,p'*-DDT+*p,p'*-DDD+*p,p'*-DDT+*p,p'*-DDE; ΣPCBs=sum of unidentified PCB congeners; ΣHCH=α+β+γ; CHL=*trans*-e+*cis*-chlordane+*trans*-+*cis*-nonachlor+oxychlordane
	JF	0.6	0.1	0.4	0.01		0.001	
	AF	0.4	0.02	0.6	0.01		0.1	
P. phocoena[14]	AF	5.7±0.5 (5.3, 6.0)	0.3±0.7 (0.2, 0.4)	7.4±3.9 (0.8-15.0)	0.4±0.1 (0.1-0.6)			ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD+*o,p'*-DDT; ΣPCBs=sum of PCB congeners identified in Kanechlor 300, 400, 500 & 600; ΣCHL=*cis*-+*trans*-chlordane+*trans*-+*cis*-nonachlor+oxychlodane; ΣHCH=α+β+γ
	JM	12.9±5.1 (5.0-24.0)	0.7±0.3 (0.2-1.1)	9.8±3.5 (5.7-16.0)	0.4±0.1 (0.3-0.6)			
	AM	19.9±5.5 (1.3-3.1)	11.5±0.7 (0.5-2.4)	10.4±4.3 (5.2-17.0)	0.4±0.1 (0.3-0.6)			
T. truncatus[15]	JF&JM	0.05 (0.02-0.1)		5.5 (3.2-8.0)	3.4 (0.3-5.7)		1.6 (0.7-2.3)	doesn't state composition of ΣPCB; ΣCHL=*cis*-chlordane+oxychlordane+heptachlor epoxide
	AF	0.01 (0.002-0.02)		0.7 (0.1-2.1)	0.3 (0.0-0.8)		0.4 (0.002-1.3)	
	AM	0.1 (0.1-0.2)		6.1 (2.9-10.9)	0.3 (0.1-0.7)		1.1 (0.3-1.8)	
S. chinensis[16]	AM	31.0 (13.0-50.0)						
Sirenians								
T. manatus latirostris[11]	JM				0.04			ΣHCB=hexachlorobenzene

Table Four(b) continued

Species	Sex/Age	ΣPCB	ΣCHL	ΣHCH	ΣHCB	Lindane	Dieldrin	Comments
T. manatus latirostris[12]	U	1.4±1.1 (0.5-4.6)	ND		ND		0.3±0.1 (0.1-0.4)	ΣDDT=*p,p'*-DDT+*p,p'*-DDE+*p,p'*-DDD; doesn't state composition of ΣPCB; ΣCHL=*cis*-chlordane+*cis*-+*trans*-nonachlor+oxychlordane+heptachlor epoxide;
Pelagic Odontocetes								
D. delphis[17]	AF	113.3±41.6 (80.0-160.0)	0.2±0.3 (ND-0.5)		0.1±0.1 (ND-0.2)		0.4±0.6 (ND-1.1)	
	AM	135.0±64.5 (80.0-300.0)	1.6±3.3 (ND-10.5)		0.1±0.1 (ND-0.3)		0.3±0.5 (ND-1.4)	
S. coeruleoalba[17]	AF	3.0±1.7 (1.2-4.8)	0.1±0.1 (ND-0.2)		0.02±0.04 (ND-0.1)		0.2±0.2 (ND-0.3)	ΣPCB=Aroclor 1254/1260; ΣCHL=*trans*-nonachlor+oxychlordane+heptachlor epoxide
	AM	5.0	0.1		0.1		ND	
L. acutus[7]	UM	34.3±14.5						
	UF	21.2±17.8						
L. borealis[16]	AM	30.0						ΣPCB=sum of 75 congeners (unstated)
G. griseus[18]	AM	1.7	0.4	0.1	0.03		0.02	
G. griseus[19]	JF	20.0						ΣDDT=*p,p'*-DDT+*p,p'*-DDE; ΣPCB= sum of congeners77, 105, 118, 126, 12, 137, 138, 153, 156, 169, 170, 180, 194
G. melas[20]	JF	47.8±29.5						
	AF	15.5±12.4						
	JM	61.4±27.3						
	AM	57.4±24.6						
P. crassidens[18]	AM	40.0±8.5 (46.0, 34.0)	6.8±0.4 (6.5, 7.1)	0.5±0.4 (0.2, 0.8)	0.3±0.3 (0.1, 0.5)		0.3±0.1 (0.3, 0.4)	ΣDDT=*p,p'*-DDE+*p,p'*-DDD+*p,p'*-DDT+*o,p'*-DDT; ΣPCB=37+81+77+126+169; ΣHCH=α+β+γ; ΣHCH=*trans*+*cis*-chlordane+*trans*-+*cis*-nonachlor+oxychlordane;
O. orca[18]	AF(1), JM(5)	22.0	3.9	0.7	0.5		0.3	Values given are geometric means
M. densirostris[21]	JM	29.0	0.30					ΣPCB=Aroclor 1260; ΣCHL=α-chlordane
	AM	14.0	0.1					

Table Four(b) continued

Species	Sex/Age	ΣPCB	ΣCHL	ΣHCH	ΣHCB	Lindane	Dieldrin	Comments
Z. cavirostris[22]	AF	9.0						ΣDDT=*p,p'*-DDT+*p,p'*-DDD+*o,p'*-DDD+*p,p'*-DDE; ΣPCB=sum of unidentified peaks from standards, extrapolation from retention times published elsewhere and using the response factors of the closest isomers
	AM	9.6±2.4 (7.9-12.3)						
P. macrocephalus[21]	AF	4.0	ND				ND	ΣPCB=Aroclor 1260; ΣCHL=α-chlordane
	AM	0.7	ND				ND	
	JM	2.3±0.6 (1.6-3.1)	1.1±0.3 (0.9-1.6)	0.1±0.0 (0.1-0.2)	0.2±0.1 (0.1-0.3)		0.3±0.1 (0.2-0.5)	ΣDDT=*p,p'*-DDT+*o,p'*-DDT+*p,p'*-DDD+*o,p'*-DDD+*p,p'*-DDE+*o,p'*-DDE; ΣPCB=sum of ICES7 congeners; ΣCHL=*trans*-chlordane+*cis*-+*trans*-nonachlor; ΣHCH=α+β+γ

All values μg g^{-1} wet weight. ND: not detected
*Source of samples: BY: bycatch; SS: scientific sampling; STR: stranding; W: whaling;
^Age/Sex: A: adult; J: juvenile; F: female; M: male; U: unknown.
[1]Vetter *et al.* 1996; [2]Newman *et al.* 1994; [3]Schantz *et al.* 1993; [4]Kurtz and Kim 1976; [5]Aono *et al.* 1997; [6]Skaare 1995; [7]Borrell 1993; [8]Béland *et al.* 1991 in O'Shea and Brownell 1994; [9]Aguilar and Borrell 1988; [10]Woodley *et al.* 1991; [11]Ames and VanVleet 1996; [12]O'Shea *et al.* 1984; [13]Kannan *et al.* 1994; [14]Tanabe *et al.* 1997; [15]Kuehl and Haebler 1995; [16]Minh *et al.* 2000; [17]O'Shea *et al.* 1980; [18]Jarman *et al.* 1996; [19]Corsolini *et al.* 1995; [20]Borrell and Aguilar 1993; [21]Taruski *et al.* 1975; [22]Knap and Jickels 1983; [23]Law *et al.* 1996

Table Five: Mean concentrations ± SD (range) of mercury cadmium, lead, copper and zinc, in the liver tissue of selected marine mammals in the Northern Hemisphere.

Species	Area	Year	Source of sample	Sex	n	Hg	Cd	Pb	Cu	Zn
Pinnipeds										
P. vitulina[1]	England	1988-89	STR/BY	JF	2	13.7±10.3 (6.4, 21.0)	0.2±0.2 (0.04, 0.3)	0.3±0.04 (0.3, 0.4)	5.9±0.1 (5.8, 6.0)	57.0±12.3 (48.0, 66.0)
				AF	5	65.6±32.0 (35.0-100.0)	0.2±0.1 (0.1-0.3)	0.3±0.04 (0.3-0.4)	8.4±2.8 (6.2-13.0)	50.4±5.7 (43.0-57.0)
				JM	5	7.8±5.2 (1.0-16.0)	0.1±0.04 (0.03-0.1)	0.3±0.03 (0.03-0.1)	9.2±2.4 (6.1-12.0)	45.0±4.6 (41.0-52.0)
				AM	4	58.9±50.2 (9.6-110.0)	0.1±0.03 (0.1-0.2)	0.4±0.03 (0.4-0.4)	6.8±0.6 (6.2-7.4)	43.3±5.1 (39.0-49.0)
P. groenlandicus[2]	Greenland Sea	1985	SS	JF&JM	6	0.3±0.2 (0.1-0.7)	0.3±0.3 (0.1-0.9)	0.1±0.04 (0.04-0.2)	16.0±15.0 (10.2-22.8)	90.0±30.0 (57.6-129.0)
				AF	15	2.0±2.0 (0.5-6.8)	14.0±6.0 (3.6-25.1)	0.1±0.1 (0.02-0.5)	13.0±6.0 (5.3-20.6)	50.0±20.0 (30.2-96.10
				AM	8	2.0±3.0 (0.35-7.70)	16.0±5.0 (9.4-22.4)	0.1±0.1 (0.0-0.3)	14.0±7.0 (6.5-29.3)	70.0±10.0 (52.1-100.0)
C. ursinus[3]	Sanriku, Japan	1990-91	SS	J&A F&M	7JM, 4JF, 1AM, 38AF	35.4±30.4 (6.1-163.0)	9.96±5.79 (2.25-33.30)		18.40±5.90 (7.46-34.10)	64.80±15.20 (26.0-95.80)
Z. c. californianus[4]	Oregon, USA	1973	SS	JM	3	95.7±24.5	1.6±0.2			
Mysticetes										
B. acutorostrata[5#]	Greenland	1980	W	JF&JM	10	0.3 (0.1-2.7)	0.9 (0.5-1.1)			35.1 (26.4-48.0)
				AF&AM	4	0.5 (0.2-0.7)	0.9 (0.5-1.5)			34.0 (32.1-38.9)
Coastal Odontocetes										
P. gangetica[7]	Ganges River, India	1988-92	BY	JF	1		0.03	<0.3	148.2	37.0
				AF	1		0.1	<0.3	3.5	23.7
				JM	2		0.03±0.02	0.4±0.4	77.8±15.7	63.0±21.0
T. tursiops[8]	Tenby, Britain	1989	STR	AF	1	20.0	0.1	<0.7	5.7	32.0
T. tursiops[8]	Cardigan Bay, Britain	1989	STR	AM	1	21.0	0.1	<0.6	8.3	42.0

Table Five continued.

Species	Area	Year	Source of sample	Sex	n	Hg	Cd	Pb	Cu	Zn
T. tursiops[9]	Gulf of Mexico	1990	STR	JF&M	5	4.4 (1.7-8.4)	0.1 (0.1-0.2)	0.3 (0.04-0.9)		
				AF	5	25.9 (6.1-48.7)	0.3 (0.1-0.6)	0.5 (0.1-1.2)		
				AM	9	45.5 (5.1-87.8)	0.4 (0.1-1.3)	0.7 (0.2-2.1)		
Sirenians										
T. manatus latirostris[6]	Florida, USA	1977-81	STR	J&A F&M	19 (Pb, Hg, Se), 35 (Fe), 54 (Cu)	ND-0.05		0.7 (0.4-1.1)	42.7 (1.1-292.7)	
Pelagic Odontocetes										
D. delphis[1]	England	1990-92	STR/BY	JF	3	2.5±2.5 (0.3-6.1)	0.4±0.3 (0.04-0.7)	0.2±0.2 (0.1-0.4)	5.5±1.2 (4.3-7.1)	36.3±4.4 (32.0-42.0)
				AF	11	21.5±29.3 (1.7-9.3)	1.9±2.9 (0.2-9.0)	0.1±0.1 (0.02-0.3)	5.0±1.8 (2.-9.60)	38.7±14.3 (21.0-67.0)
				JM	2	2.6±3.4 (0.2, 5.0)	0.1±0.1 (<0.1, 0.2)	0.1±0.1 (0.1, 0.1)	6.0±3.4 (3.6, 8.)	41.0±7.1 (36.0, 46.0)
				AM	7	21.2±22.5 (2.2-67.0)	0.5±0.4 (0.1-1.0)	0.1±0.03 (0.04-0.1)	5.0±0.9 (4.207.0)	33.3±6.1 (24.0-42.0)
S.attenuata[12]	Eastern Tropical Pacific	1977-83	BY	JF	4	2.0±2.0 (0.2-4.0)				
				AF	24	75.3±51.0 (13.6-217.5)				
				JM	5	8.9±7.6 (0.2-17.7)				
				AM	11	81.8±51.9 (29.0-183.1)				
S. coeruleoalba[10]	Tajii, Japan	1978	SS	AF	1		7.0	0.1	8.0	35.3
				AM	1		2.1	0.1	9.3	35.5
S. coeruleoalba[11]	Mediterranean Sea, France	1972-80	STR	JF	3	134.1±172.8 (20.4-333.0)				
				AF	10	516.8±450.3 (4.7-1544.0)				
				JM	4	161.6±318.2 (1.2-639.0)				
				AM	8	304.4±200.5 (108.0-733.0)				

Table Five continued.

Species	Area	Year	Source of sample	Sex	n	Hg	Cd	Pb	Cu	Zn
L. albirostris[18]	Newfoundland	1982	STR	UF&M	27 (Hg, Pb, Zn), 26 (Cd), 24 (Cu)	1.1 (0.2-2.2)	0.9 (0.1-3.1)	0.2 (0.01-0.5)	7.5 (1.3-11.9)	36.9 (16.1-50.4)
G. griseus[13]	Argyll, Scotland	1986	STR	JF	1	1.2±0.02				
G. griseus[14]	Korea	2000	BY	JM	1		0.2	<0.03	1.0	29.9
G. macrorhynchus[15]	Georgia, USA	1977	STR	AF	3	289.0±18.7	14.8±1.1			
				AM	1	56.9±3.8	11.3±0.1			
G. melas[16]	Faroe Islands	1987	W	AF	18	119.6±59.0	62.3±19.1		7.6±1.4	67.9±14.7
				AM	10	76.4±28.4	33.1±17.9		5.3±0.8	72.2±26.1
P. macrocephalus[19]	North Sea	1995	STR	JM	1	34.0	30.0	0.1	2.3	34.0
P. macrocephalus[20]	North Sea	1994-95	STR	AM	7	23.3±14.9 (2.8-42.6)	30.8±14.4 (16.8-56.5)	0.5±0.4 (0.2-1.0)	2.7±0.9 (1.7-3.8)	33.7±4.7 (29.0-40.3)

All values μg g^{-1} wet weight.
*Source of samples: BY: bycatch; SS: scientific sampling; STR: stranding; W: whaling;
^Age/Sex: A: adult; J: juvenile; F: female; M: male; U: unknown.
#Values given are medians and ranges.
Conversion factors (dry wt: wet wt): *P. gangetica*: 2.7:1 (small odontocetes in Law 1994); *T. manatus latirostris*: 4.1:1 (*D. dugong* in Denton *et al.* 1980); *L. albirostris*: 2.7:1 (*Lagenorhynchus* spp. in Law 1994); *P. macrocephalus*: 3.1:1 (Law *et al.* 1996).
[1]Law 1994; [2]Julshamn and Grahl Nielsen 2000; [3]Noda *et al.* 1995; [4]Buhler *et al.* 1975; [5]Hansen *et al.* 1990; [6]O'Shea *et al.* 1984; [7]Kannan *et al.* 1993; [8]Law *et al.* 1991; [9]Kuehl and Haebler 1995; [10]Honda *et al.* 1982; [11]Andre *et al.* 1991; [12]Andre *et al.* 1990; [13]Zonfrillo *et al.* 1987; [14]Gu Choi *et al.* 2000; [15]Stoneburner 1978; [16]Caurant *et al.* 1993; [17]Caurant *et al.* 1994; [18]Muir *et al.* 1988; [19]Law *et al.* 1996; [20]Holsbeek *et al.* 1999.

Table Six: Mean concentrations ± SD (range) of mercury cadmium, lead, copper and zinc, in the kidney tissue of selected marine mammals in the Northern Hemisphere.

Species	Area	Year	Source of sample	Age/Sex^	N	Hg	Cd	Pb	Cu	Zn
Pinnipeds										
P. groenlandicus[2]	Greenland Sea	1985	SS	JF&M	6	0.2±0.2 (0.1-0.5)	0.6±0.5 (0.1-1.3)	0.1±0.1 (0.1-0.2)	4.3±0.4 (3.9-5.0)	40.0±20.0 (22.7-76.8)
				AF	15 except Pb (13)	0.7±0.6 (0.1-2.3)	50.0±20.0 (24.2-101.0)	0.2±0.1 (0.1-0.3)	6.0±2.0 (3.9-9.9)	50.0±10.0 (32.0-68.7)
				AM	8	0.7±0.4 (0.3-1.3)	50.0±20.0 (27.2-94.1)	0.1±0.1 (0.1-0.3)	5.0±2.0 (2.9-7.7)	50.0±10.0 (30.9-66.9)
C. ursinus[3]	Sanriku, Japan	1990-91	SS	J&A F&M	7JM, 4JF, 1AM, 38AF	1.2±0.4 (0.6-2.6)	45.4±20.4 (12.4-111.0)		5.7±1.3 (3.8-11.3)	46.6±8.6 (27.6-78.8)
Z. c. californianus[4]	Oregon, USA	1973	SS	JM	3	5.4±4.7	7.2±2.7			
Mysticetes										
B. acutorostrata[5]	Greenland	1980	W	JF&M	10	0.3 (0.2-1.2)	4.1 (3.7-5.1)			19.2 (18.2-19.4)
				AF&M	4	0.3 (0.2-0.6)	3.3 (1.7-5.6)			21.5 (15.2-26.1)
Coastal Odontocetes										
P. gangetica[7]	Ganges River, India	1988-92	BY	JF	1		<0.02	0.5	5.4	11.5
				AF	1		2.7	<0.3	5.4	11.5
				JM	2		0.03±0.02	0.8±0.2	19.2±11.8	52.1±8.8
Sirenians										
T. manatus latirostris[6]	Florida, USA	1977-81	STR	UF&M	38 (Cd), 20 (Pb)		4.9±8.2 (ND-36.5)	1.0±0.2 (0.6-1.4)		
Pelagic Odontocetes										
D. delphis[1]	England	1990-92	STR/BY	JF	1	0.3	2.6	0.1	2.7	16.0
				AF	5	1.7±1.2 (0.9-3.5)	1.9±1.1 (0.03-3.0)	0.03±0.02 (0.03-3.0)	2.6±0.6 (1.9-3.40	16.6±3.9 (12.0-22.0)
				AM	4	1.5±0.9 (0.5-2.7)	3.4±3.9 (1.1-9.3)	0.03±0.02 (0.02-0.1)	2.7±0.3 (2.5-3.1)	18.0±1.8 (16.0-20.0)
S.attenuata[12]	Eastern Tropical Pacific	1977-83	BY	JF	4	0.6±0.6 (0.1-1.5)				
				AF	24	6.3±2.5 (2.3-12.8)				

Table Six continued.

Species	Area	Year	Source of sample*	Age/Sex^	N	Hg	Cd	Pb	Cu	Zn
S.attenuata[12]	Eastern Tropical Pacific	1977-83	BY	JM	5	2.8±3.2 (0.1-7.9)				
				AM	11	5.6±3.1 (0.4-12.0)				
S. coeruleoalba[10]	Tajii, Japan	1978	SS	AF	1		63.7	0.2	3.2	27.7
				AM	1		9.2	0.2	3.2	24.0
S. coeruleoalba[11]	Mediterranean Sea, France	1972-80	STR	JF	3	12.4±9.1 (4.7-22.5)				
				AF	11	61.0±56.7 (3.1-178.9)				
				JM	4	7.6±11.1 (1.4-24.2)				
				AM	9	25.5±12.3 (12.0-49.0)				
L. albirostris[18]	Newfoundland	1982	STR	UF&M	25 except Cu (23)	0.5 (0.0-0.9)	5.9 (1.1-19.0)	0.3 (0.004-0.9)	6.8 (4.4-11.8)	36.9 (29.7-48.7)
G. griseus[13]	Argyll, Scotland	1986	STR	JF	1	0.6±0.1				
G. griseus[14]	Korea	2000	BY	JM	1		0.03	<0.03	0.8	17.3
G. macrorhynchus[15]	Georgia, USA	1977	STR	AF	3	30.8±1.8	32.6±2.3			
				AM	1	4.8±1.0	27.8±1.7			
G. melas[17]	Faroe Islands	1987	W	J&A F&M	31	4.9±3.8	55.0±20.0		3.8±1.0	35.0±4.4
M. stejnegeri[14]	Samchok, Korea	1999-2000	STR/BY	AF	2		0.2	<0.03	1.6	12.9
P. macrocephalus[20]	North Sea	1994-95	STR	AM	6	4.1±2.0 (1.4-6.5)	83.2±37.2 (42.9-137.4)	0.4±0.4 (0.2-1.2)	6.4±4.4 (4.2-14.2)	30.39±11.3 (14.2-45.2)

All values μg g^{-1} wet weight.
*Source of sample: BY: bycatch; SS: scientific sampling; STR: stranding; W: whaling;
^Age/Sex: A: adult; J: juvenile; F: female; M: male; U: unknown.
#Values given are median and range.
Conversion factors (dry wt: wet wt): *P. gangetica*: 2.4:1 (small odontocetes in Law 1994); *T. manatus latirostris*: 5.2:1 (*D. dugong* in Denton *et al.* 1980); *L. albirostris*: 2.3:1 (*Lagenorhynchus* spp. in Law 1994); *P. macrocephalus*: 3.1:1 (Law *et al.* 1996).
[1]Law 1994; [2]Julshamn and Grahl Nielsen 2000; [3]Noda *et al.* 1995; [4]Buhler *et al.* 1975; [5]Hansen *et al.* 1990; [6]O'Shea *et al.* 1984; [7]Kannan *et al.* 1993; [8]Law *et al.* 1991; [9]Kuehl and Haebler 1995; [10]Honda *et al.* 1982; [11]Andre *et al.* 1991; [12]Andre *et al.* 1990; [13]Zonfrillo *et al.* 1987; [14]Gu Choi *et al.* 2000; [15]Stoneburner 1978; [16]Caurant *et al.* 1993; [17]Caurant *et al.* 1994; [18]Muir *et al.* 1988; [19]Law *et al.* 1996; [20]Holsbeek *et al.* 1999.

LIST OF FIGURES

Figure One

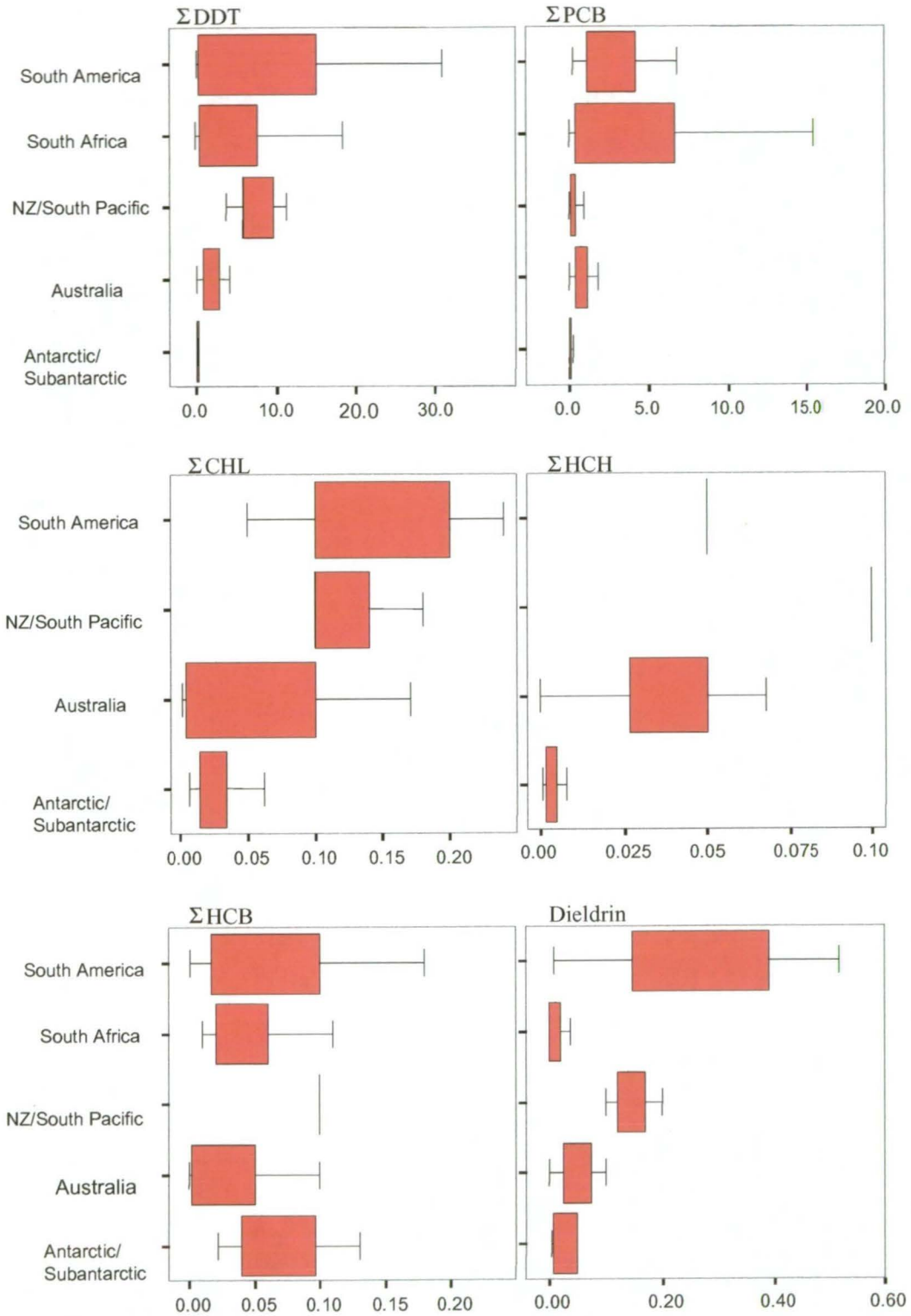

ΣDDT
ΣPCB
South America
South Africa
NZ/South Pacific
Australia
Antarctic/
Subantarctic
0.0
10.0
20.0
30.0
0.0
5.0
10.0
15.0
20.0
ΣCHL
ΣHCH
South America
NZ/South Pacific
Australia
Antarctic/
Subantarctic
0.00
0.05
0.10
0.15
0.20
0.00
0.025
0.05
0.075
0.10
ΣHCB
Dieldrin
South America
South Africa
NZ/South Pacific
Australia
Antarctic/
Subantarctic
0.00
0.05
0.10
0.15
0.20
0.00
0.20
0.40
0.60

Figure Two

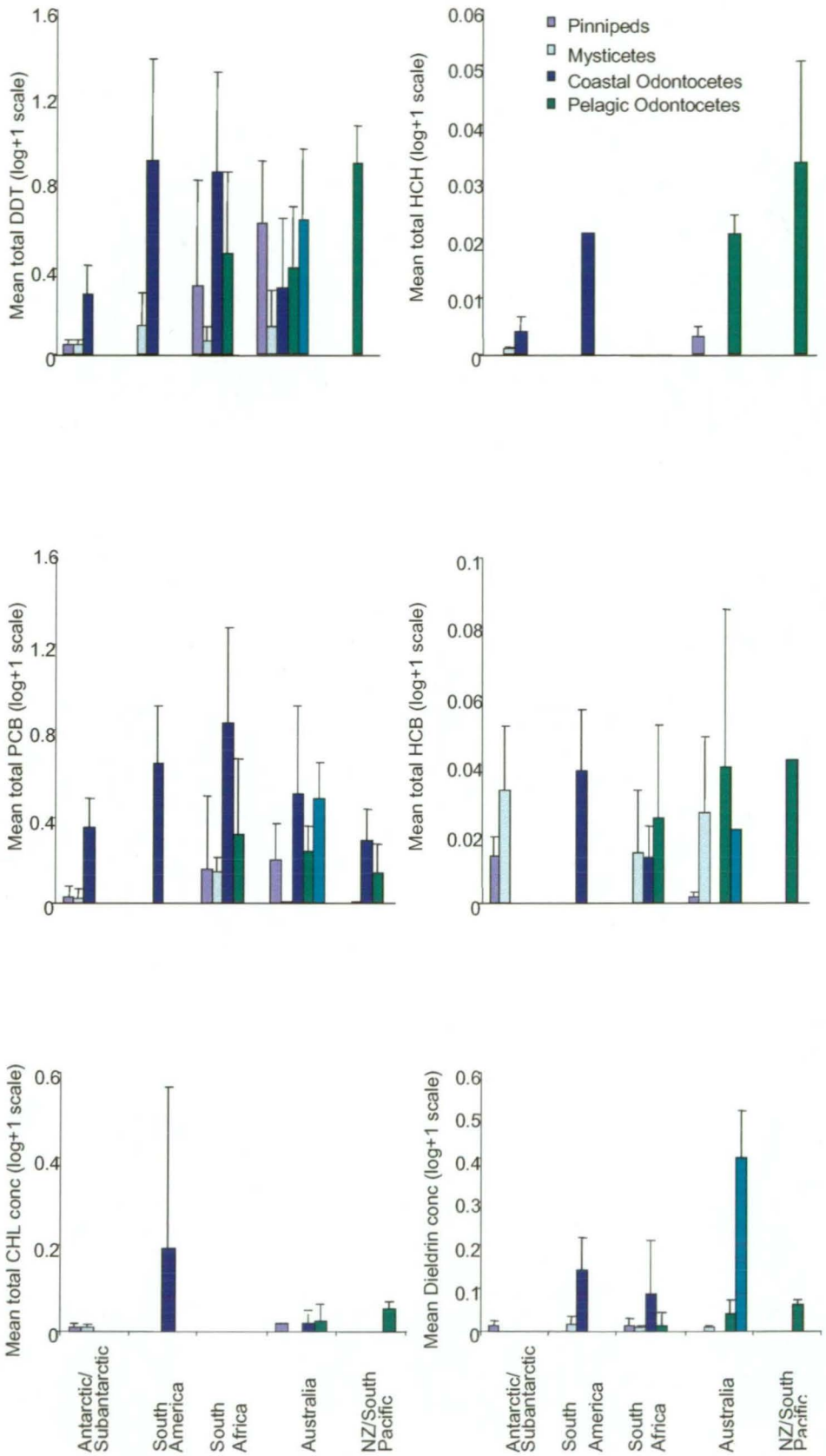
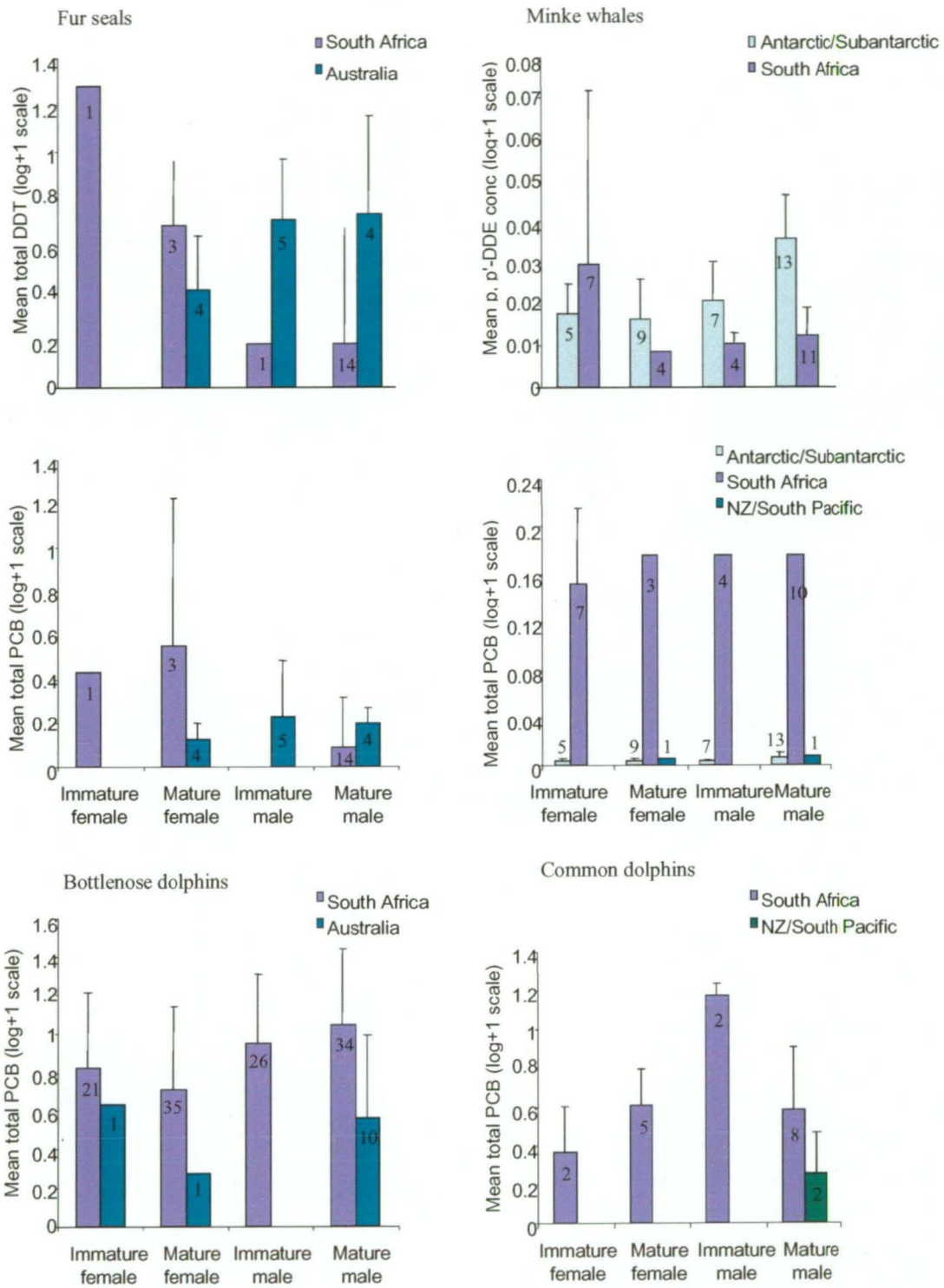
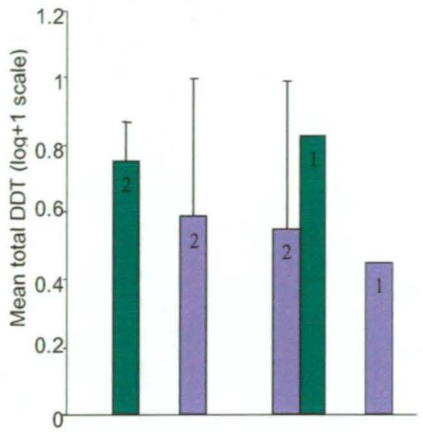

Mean total DDT (log+1 scale)
Mean total HCH (log+1 scale)
Pinnipeds
Mysticetes
Coastal Odontocetes
Pelagic Odontocetes
Mean total PCB (log+1 scale)
Mean total HCB (log+1 scale)
Mean total CHL conc (log+1 scale)
Mean Dieldrin conc (log+1 scale)
Antarctic/ Subantarctic
South America
South Africa
Australia
NZ/South Pacific

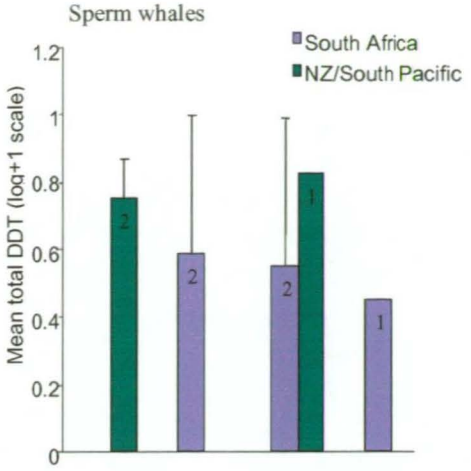
Figure Three

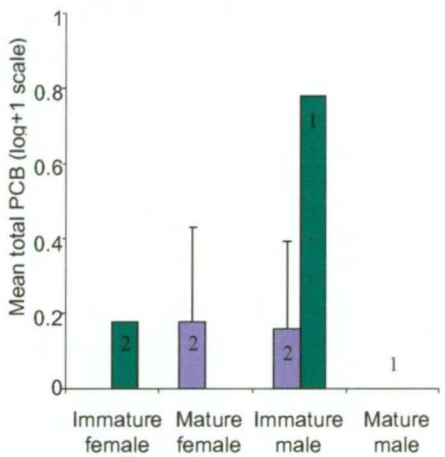


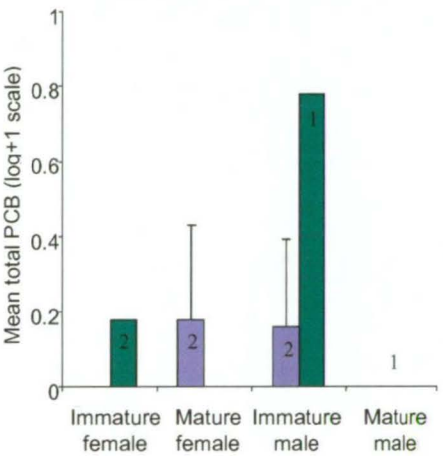
Striped dolphins



Sperm whales







Dusky dolphins

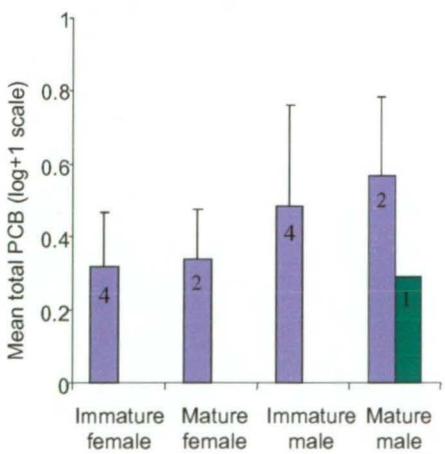


Figure Four

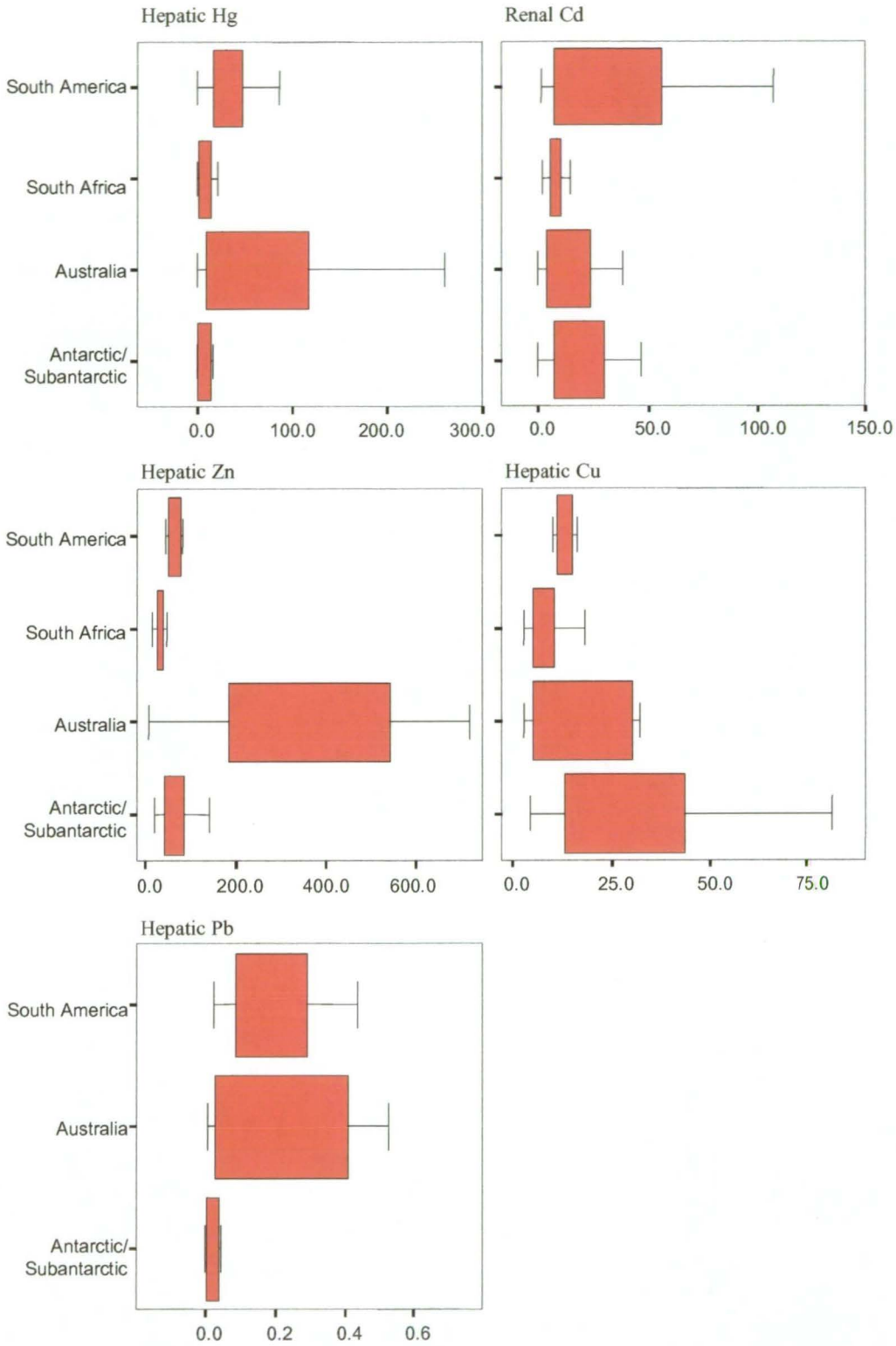

Hepatic Hg
South America
South Africa
Australia
Antarctic/
Subantarctic
0.0
100.0
200.0
300.0
Renal Cd
0.0
50.0
100.0
150.0
Hepatic Zn
South America
South Africa
Australia
Antarctic/
Subantarctic
0.0
200.0
400.0
600.0
Hepatic Cu
0.0
25.0
50.0
75.0
Hepatic Pb
South America
Australia
Antarctic/
Subantarctic
0.0
0.2
0.4
0.6

Figure Five

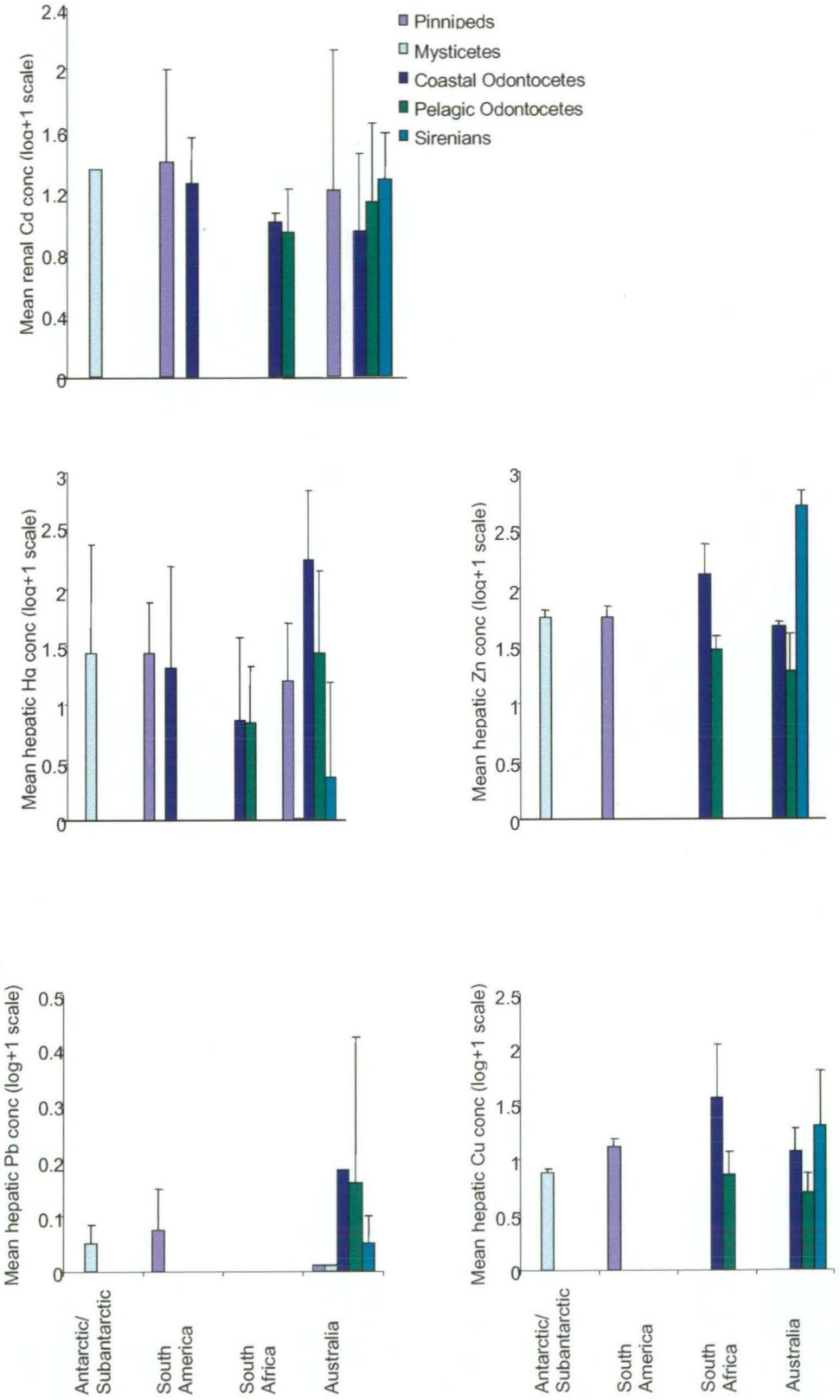
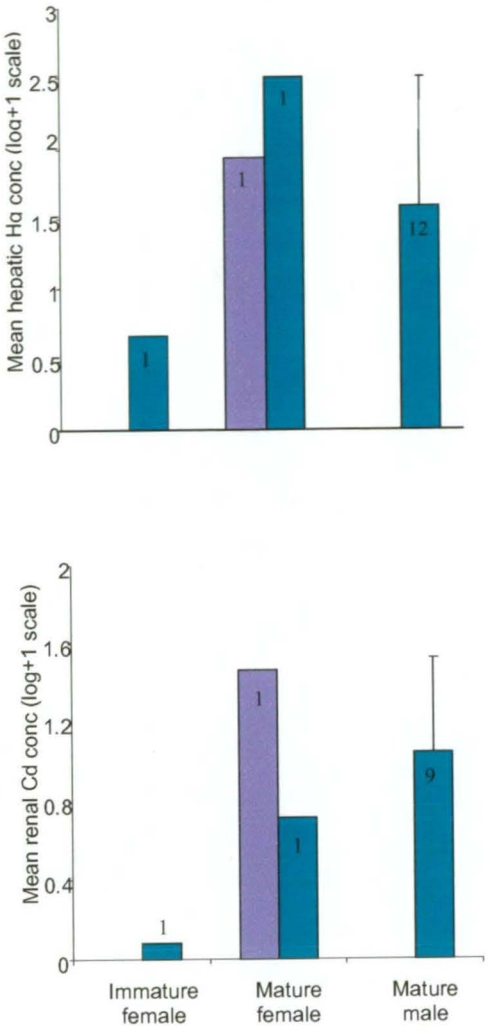

Mean renal Cd conc (log+1 scale)
2.4
2
1.6
1.2
0.8
0.4
0
Pinnipeds
Mysticetes
Coastal Odontocetes
Pelagic Odontocetes
Sirenians
Mean hepatic Hg conc (log+1 scale)
3
2.5
2
1.5
1
0.5
0
Mean hepatic Zn conc (log+1 scale)
3
2.5
2
1.5
1
0.5
0
Mean hepatic Pb conc (log+1 scale)
0.5
0.4
0.3
0.2
0.1
0
Antarctic/ Subantarctic
South America
South Africa
Australia
Mean hepatic Cu conc (log+1 scale)
2.5
2
1.5
1
0.5
0
Antarctic/ Subantarctic
South America
South Africa
Australia

Figure Six


Mean hepatic Hg conc (log+1 scale)
3
2.5
2
1.5
1
0.5
0
1
1
1
12
Mean renal Cd conc (log+1 scale)
2
1.6
1.2
0.8
0.4
0
1
1
1
9
Immature female
Mature female
Mature male

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. Behavioural and Brain Sciences 24(2): 346-347.

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Mesnick, S. L., Evans, K. Taylor, B. L., Hyde, J., Escorza-Trevino, S., and A. E. Dizon. Sperm whale social structure: why it takes a village to raise a child (2003) Pages 170-174 in B. M. d. Wall and P. L. Tyack (eds.). Animal social complexity. Intelligence, culture and individualized societies. Harvard University Press, New York.

Animal Social Complexity

Intelligence, Culture, and Individualized Societies

EDITED BY

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